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Oocytes, Eggs, and Ovarioles of Some Long-Tongued Bees (Hymenoptera: Apoidea)

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Appendix: *Parammobatodes rozeni*, a New Bee Species from Israel, by Maximilian Schwarz[3]

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ABSTRACT

We present here new information regarding the number of ovarioles and the number and size of mature oocytes of certain bee taxa collected on a field trip in Turkey in June and July 2001. This information is augmented with similar data concerning taxa related at the tribal level to those that we found in Turkey. The mature oocytes/eggs of all taxa listed below are described and most are illustrated by photographs, scanning electron micrographs, and/or line drawings, and comparisons are made with previously published descriptions.

These taxa, arranged by family, subfamily, and tribe, are as follows: **MEGACHILIDAE: Megachilinae: Dioxyini:** *Dioxys cincta* (Jurine), *Dioxys pacificus* Cockerell. **APIDAE: Xylocopinae: Xylocopini:** *Xylocopa* (*Proxylocopa*) *olivieri* Lepeletier**; Nomadinae: Ammobatoidini:** *Holcopasites insoletus* (Linsley), *Holcopasites tegularis* Hurd and Linsley; **Nomadinae: Biastini:** *Biastes brevicornis* (Panzer); **Nomadinae: Ammobatini:** *Ammobates carinatus* Morawitz, *Parammobatodes rozeni* Schwarz, *Oreopasites* (*Oreopasites*) *favreauae* Rozen, *Oreopasites* (*Oreopasites*) *vanduzeei* Cockerell, *O.* (*Perditopasites*) *barbarae* Rozen, *O.* (*P.*) *linsleyi* Rozen, "*Parammobatodes*" *orientana* (Warnke), *Pasites maculatus* Jurine, *Sphecodopsis* (*Pseudodichroa*) *capensis* (Friese), *S.* (*P.*) *fumipennis* (Bischoff); **Apinae: Melectini:** *Melecta albifrons albovaria* Erichson, *Melecta* species, *Thyreomelecta kirghisia* Rightmyer and Engel, *Thyreus lieftincki* Rozen, *Xeromelecta californica* (Cresson).

The mature oocyte of *Xylocopa* (*Proxylocopa*) *olivieri*, a ground-nesting species, is found to be large relative to the body size of the female but somewhat smaller than the "giant" eggs of wood-nesting *Xylocopa*, as classified by Iwata and Sakagami (1966. Gigantism and dwarfism in bee eggs in relation to the mode of life, with notes on the number of ovarioles. Japanese Journal of Ecology 16: 4–16). Egg deposition habits of some cleptoparasitic taxa are discussed. In addition to smaller size relative to body size, eggs of cleptoparasitic bees show great variation in micropylar structure, dimensions, and chorionic ornamentation, thickness, and patterning, compared with eggs of nonparasitic bees.

An appendix by Maximilian Schwarz describes and names *Parammobatodes rozeni*, new species, from Israel.

ÖZET

Haziran ve Temmuz 2001'de Türkiye'den toplanan bazı arı türleri üzerinde yapılan çalişmalarda bunlardaki yumurtalık sayısı, olgun oosit sayısı ve büyüklükleri incelenmiş ve elde edilen yeni bulgular, tribus düzeyinde ilgili taxa ile karşılaştırılmıştır. Aşağıda sıralanan taxa'nın olgun oosit ve yumurtaları tanılanmış, çoğunun fotoğraf, skenin elektron mikrograf ve çizimleri yapılarak daha önceki çalışmalarla karşılaştırılmıştır.

Bu taxa; familya, altfamilya ve tribus olarak aşağıdaki şekilde sıralanmıştır: **MEGACHILIDAE: Megachilinae: Dioxyini:** *Dioxys cincta* (Jurine), *Dioxys pacificus* Cockerell. **APIDAE: Xylocopinae: Xylocopini:** *Xylocopa* (*Proxylocopa*) *olivieri* Lepeletier; **Nomadinae: Ammobatoidini:** *Holcopasites insoletus* (Linsley), *Holcopasites tegularis* Hurd and Linsley; **Nomadinae: Biastini:** *Biastes brevicornis* (Panzer); **Nomadinae: Ammobatini:** *Ammobates carinatus* Morawitz, *Parammobatodes rozeni* Schwarz, *Oreopasites* (*Oreopasites*) *favreauae* Rozen, *Oreopasites* (*O.*) *vanduzeei* Cockerell, *O.* (*Perditopasites*) *barbarae* Rozen, *O.* (*P.*) *linsleyi* Rozen, "*Parammobatodes*" *orientana* (Warnke), *Pasites maculatus* Jurine, *Sphecodopsis* (*Pseudodichroa*) *capensis* (Friese), *S.* (*P.*) *fumipennis* (Bischoff); **Apinae: Melectini:** *Melecta albifrons albovaria* Erichson, *Melecta* türleri, *Thyreomelecta kirghisia* Rightmyer and Engel, *Thyreus lieftincki* Rozen, *Xeromelecta californica* (Cresson).

Toprakta yuva yapan *Xylocopa* (*Proxylocopa*) *olivieri*'nin olgun oositinin dişinin iri yapılı vücuduna uyumlu olarak büyük olduğu saptanmış, ancak Iwata ve Sakagami (1966)'nın "dev" olarak sınıflandırdığı odunlarda yuva yapan *Xylocopa* türlerinin yumurtalarından küçük olduğu dikkati çekmiştir. Bazı kleptoparazitik yaşam sürdüren türlerin yumurta koyma davranışları tartışılmış, diğer arı türlerininki ile karşılaştırıldıklarında; bunlarda vücut büyüklüğüne oranla yumurtalar daha küçük olduğu gibi, mikrofil yapısı, büyüklük, yumurta kabuğunun yüzeyindeki desenlenme, kalınlık ve şekil yönünden de büyük varyasyonlar gösterdiği belirlenmştir.

Çalışmanın ek kisminda İsrail'den toplanmış, Maximilian Schwarz tarafından tanımı yapılan ve *Parammobatodes rozeni* olarak isimlendirilen yeni tür yer almaktadır.

INTRODUCTION

On a field trip in Turkey in June and July 2001, we collected and preserved in Kahle's solution females of a number of bees whose mature oocytes and ovariole numbers might shed light on the relationship of egg size, egg morphology, and ovariole number to the biology of the bees. Subsequently, the preserved specimens were dissected so that ovarioles and mature oocytes could be counted and the follicular tissue removed from the mature oocytes to reveal their shape and chorionic structures. This paper describes and discusses these matters with respect to two kinds of bees in the Megachilidae and Apidae: cleptoparasitic taxa and the solitary, ground-nesting taxon *Xylocopa* (*Proxylocopa*), whose close relatives nest in wood. In addition to Turkish bees, this study treats related, non-Turkish taxa in the Dioxyini, Biastini, Ammobatini, and Melectini about which little has been previously reported. The ammobatoidine genus *Ammobatoides* occurs in Turkey, and several species were encountered on the field trip. Because the egg and mature oocyte of *A. abdominalis* (Eversmann) were recently described (Rozen, 2001), they are not dealt with here, but the mature oocytes of the North American ammobatoidine genus *Holcopasites* are described.

Also as a result of this field trip, we observed the egg deposition habits of an unknown species of *Melecta*, which are recorded here with a description of its egg. This description is included with the descriptions of mature oocytes of other Melectini.

METHODS, TERMS, AND OTHER PRELIMINARY CONSIDERATIONS

Early papers by Iwata (1955, 1960, 1965) and Iwata and Sakagami (1966) pioneered the examination of egg size and ovariole count related to life-styles of bees. Almost simultaneously Michener and coworkers illustrated and described ovaries and eggs of halictine and allodapine bees (Michener and Lange, 1958a, 1958b, 1959; Michener and Wille, 1961; Michener, 1962, 1971, 1973; Michener et al., 1971; Maeta et al., 1985). While they used this information mostly for understanding the social arrangements of these bees, ovariole number, egg size and shape, and oocyte number and size were often provided. A subsequent series of studies has further explored ovariole number, number of mature oocytes per ovary, egg size, and egg anatomy with special reference to parasitic bees (in order of publication: Rozen, 1986a; Alexander and Rozen, 1987; Rozen, 1989, 1992; Rozen and Roig-Alsina, 1991; Rozen and McGinley, 1991; Rozen, 1994a, 1994b; Roig-Alsina and Rozen, 1994; Alexander, 1996; Rozen et al., 1997; Rozen, 1997, 2001; Garófalo and Rozen, 2001; Alves-dos-Santos et al., 2002). Information presented here will be incorporated with a worldwide review and analysis of these matters with respect to cleptoparasitic bees (Rozen, in press).

The following descriptions employ the egg size classification used by Iwata and Sakagami (1966: table 2) based on dividing the length of the largest mature oocyte (E) by the maximum distance between the outer rims of the female's tegulae (M) to give the egg index (E/M). This classification is as follows: **dwarf** ($E/M \leq 0.50$), **small** ($0.50 < E/M \leq 0.75$), **medium** ($0.75 < E/M \leq 1.00$), **large** ($1.00 < E/M \leq 1.10$), **giant** ($1.10 < E/M$).

Partly because of this study, we conclude that the small, discrete, multipored projection arising from the anterior part of the chorion of many nomadine bee eggs is actually the micropylar process. Such projections have been termed "nipple" (Iwata, 1960: figs. 23, 24), "hooklike projection" (Rozen et al., 1997: fig. 20), and "pedunculate process" (Rozen, 2001: figs. 5, 6). The cluster of angular pores at the anterior poles of mature oocytes/eggs leaves no doubt of the homologies of these openings among the taxa treated here whether or not they are on projecting processes. Because of the thick, lenselike quality of the chorion of *Biastes brevicornis*, the micropylar duct can be seen leading to the interior portion of the egg under stereoscopic examination while the oocyte is submerged in ethanol (fig. 19). The single-pored micropyles of the ammobatines *Parammobatodes rozeni* (fig. 38), "*Parammobatodes*" *orientana* (fig. 42), and *Pasites maculatus* (fig. 47) are seemingly derived features considering the widespread multipored condition

found throughout the Apidae (including other Nomadinae), as well as in *Dioxys*.

Because oocytes are difficult to remove from the follicular tissue, they often cannot provide an impression of overall shape of mature oocytes because of either damage resulting from dissection or residual follicular tissue. Primarily for that reason, line diagrams are presented of the oocytes of some of the species described here. Micrographs of dissected oocytes taken with a scanning electron microscope (SEM) provide details, particularly of surface microstructure and the micropylar area.

The mature oocyte/egg is here considered to consist of the ovum and the chorion that surrounds it. The ovum in all preserved mature oocytes is white or nearly white; any color exhibited by the oocyte comes from the chorion. Mature oocytes of most bees possess a chorion so thin that the oocytes appear whitish, but with many parasitic bees, as demonstrated here, the chorion is thick. The term "glassy" is used to refer to chorions that are so thick that they reflect light from their inner surfaces, as do lenses. This feature was noticed especially in the mature oocytes of *Dioxys cincta* (figs. 5, 6) and *Biastes brevicornis* (figs. 16, 19), but was exhibited only when the specimens were in alcohol. After critical-point drying, vitreousness was reduced and surface textures of the chorions were revealed. This suggests that, when alive and in situ in host nest cells, these eggs may appear more like the critical-point-dried specimens than those in ethanol. In the case of *Dioxys cincta*, the micropylar area could scarcely be detected when the mature oocyte was submerged in 75% ethanol, but was immediately detected, even under moderately low magnification, after critical-point drying. Thus, the medium in which mature oocytes or eggs are viewed may be an important consideration in examining and describing them. After coating with gold palladium and viewing with the scanning electron microscope, only shape and surface features can be observed; chorionic transparency and vitrescence are totally lost (figs. 3, 4, 18).

In the following descriptions, such phrases as "under stereoscopic examination" refer to examination through a stereoscopic dissecting microscope; "under SEM examination" means examination with the use of a scanning electron microscope.

Table 1 summarizes the data on the egg index, total number of mature oocytes, oocytes per ovariole, and number of ovarioles (ovarian formula) for the species treated in this paper.

Dissected specimens and their oocytes examined for this study are preserved in the American Museum of Natural History. Other specimens collected on the field trip are both in the American Museum and in the collections of the Department of Plant Protection, Atatürk University, Erzurum, Turkey.

Megachilidae: Megachilinae: Dioxyini

The mature oocyte/egg shape and chorionic features of *Dioxys cincta* (Jurine), described below, are remarkably different from those *D. pacificus* (also described below) and *D. pomonae pomonae* (Rozen and Favreau, 1967), both North American species whose eggs/oocytes resemble those of most solitary bees. The mature oocytes/eggs of these North American species are relatively large. The average egg index of *D. pacificus* is 0.77 based on this study and that of Alexander and Rozen (1987), and the index of *D. p. pomonae* is 0.66 (as calculated under Remarks in the treatment of *D. pacificus*), both contrasting with the egg index of 0.39 for *D. cincta*, a bee that is widespread in Turkey (Özbek and van der Zanden, 1993).

Dioxys cincta (Jurine)

We presume that the surface bearing the thick, nodular chorion is dorsal and that the thin, smooth chorion typical of most bee eggs is ventral. The mature oocytes of this species tend to be variably misshaped because the anterior end at least on some specimens is obliquely pressed (in some cases, nearly side by side) against the preceding oocyte in the ovariole; figures 1–6 illustrate specimens that seemed less modified than others and had nearly full chorionic development.

Mature Oocyte (figs. 1–6): Length 1.00–1.38 mm; maximum width, lateral view 0.40–0.58 mm; maximum width, dorsal view, 0.40–0.73 mm (N = 12); egg index 0.39 (dwarf). Shape bilaterally symmetrical;

TABLE 1

Comparative Data on Number and Sizes of Mature Oocytes/Eggs and Number of Ovarioles of Bees Treated in This Study

(Taxa arranged by family and subfamily according to Michener [2000]. Numbers in the first three columns are means if more than one specimen was examined.)

Taxon	Egg index	Total no. mature oocytes	Mature oocytes per ovariole	No. ovarioles	No. specimens
MEGACHILIDAE					
MEGACHILINAE					
DIOXYINI					
Dioxys cincta (Jurine)	0.39	7	1.17	3:3	4
Dioxys pomonae pomonae Cockerell	0.66[a]	—	—	—	—
Dioxys pacificus Cockerell	0.78	1.25	0.18	3:3	4
APIDAE					
XYLOCOPINAE					
Xylocopa (*Proxylocopa*) *olivieri* Lepeletier	1.09	1	0.125	4:4	1
NOMADINAE					
AMMOBATOIDINI					
Holcopasites insoletus (Linsley)	0.27	4	0.40	5:5	1
H. tegularis Hurd & Linsley	0.45	4	0.40	5:?5	1
BIASTINI					
Biastes brevicornis (Panzer)	0.18	32	1.60	~10:10	1
AMMOBATINI					
Ammobates carinatus Morawitz	0.47	6	0.50	6:6	1
Oreopasites (*Oreopasites*) *vanduzeei* Cockerell	0.35	11.5	0.80[b]	5:5[b]	2
O. (*Perditopasites*) *barbarae* Rozen	0.63	8	0.80	5:5	2
O. (*P.*) *linsleyi* Rozen	0.60	5	0.50	5:5	1
Parammobatodes rozeni Schwarz	0.41	7	0.58	6:6	1
"*Parammobatodes*" *orientana* (Warnke)	0.52	8.5	1.06	4:4	2
Pasites maculatus Jurine	0.47	13	1.44 or 1.63	4:4 or 4:5	1
Sphecodopsis (*Pseudodichroa*) *capensis* (Friese)	0.72[c]	—	—	—	—
S. (*P.*) *fumipennis* (Bischoff)	0.67[c]	—	—	—	—
APINAE					
MELECTINI					
Melecta albifrons albovaria Erichson	0.59	3	0.38	4:4	3
Thyreomelecta kirghisia Rightmyer & Engel	0.68	4	0.50	4:4	1
Thyreus lieftincki Rozen	0.82–0.84[d]	—	—	—	—
Xeromelecta californica (Cresson)	0.59	5.33	0.67	4:4	3[e]

[a] See Remarks under *Dioxys pacificus* for method of calculating egg index of this species.

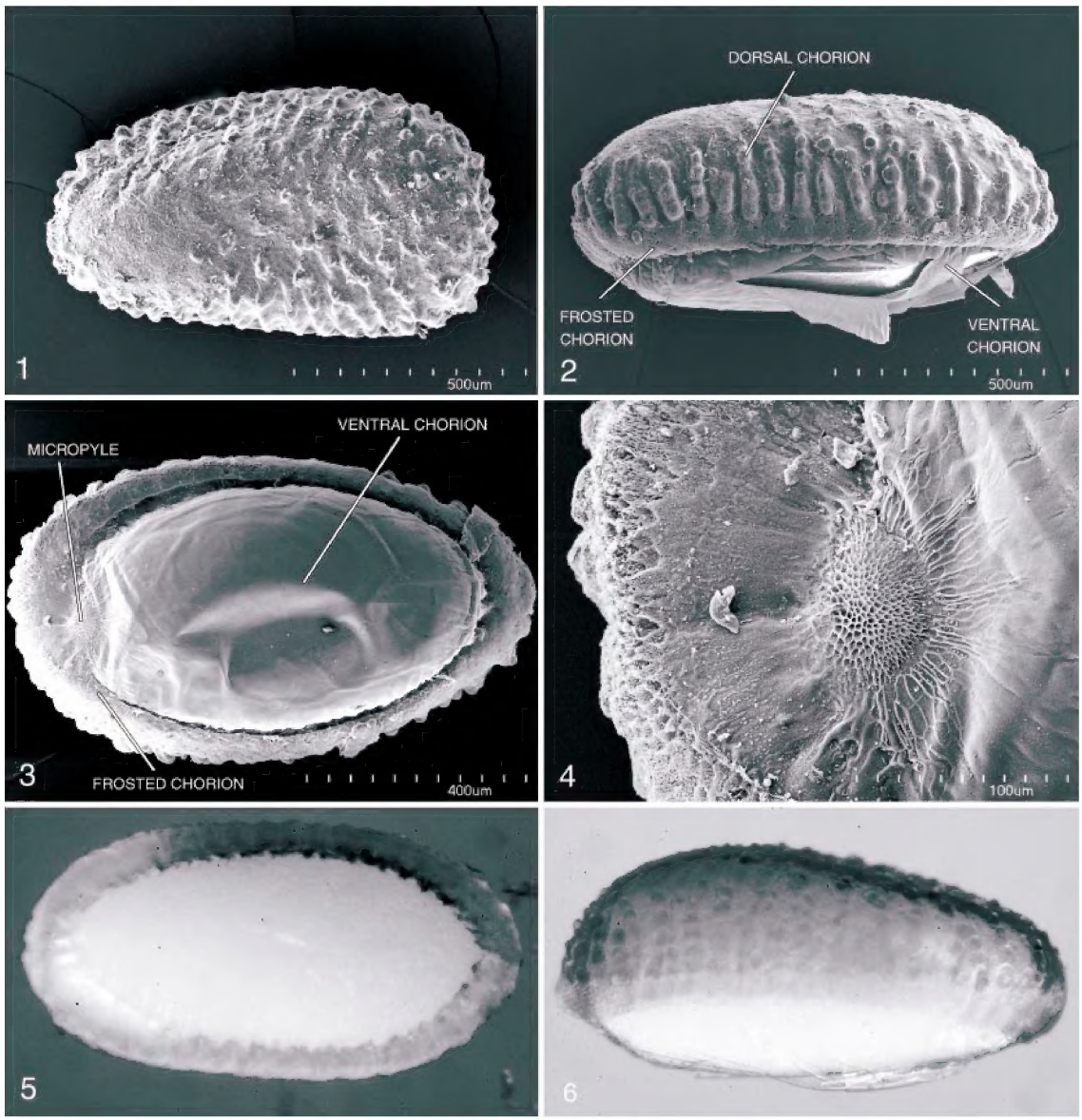
[b] Based on a single specimen.

[c] See discussions of each species of *Sphecodopsis* for method of calculating their egg indices.

[d] See discussion of *Thyreus lieftincki* for method of calculating egg index.

[e] A fourth specimen had no mature oocytes and presumably had just emerged from the pupal stage.

long axis presumably straight; maximum width, dorsal view, either anterior or posterior to midpoint; either front end or rear end more broadly rounded than opposite end; dorsal surface of egg extending over ventral surface because of thickness of dorsal chorion as seen in lateral view; micropyle at center of elevated radiating lines close to anterior edge of ventral surface (fig. 3); under SEM examination, micropyle consisting of numerous closely grouped pores (fig. 4). Ovum seemingly symmetrical along its axis, rounded at both ends. Dorsal chorion extremely thick on fully developed oocyte



Figs. 1–6. **1–4.** SEM micrographs of mature oocytes of *Dioxys cincta*, anterior ends facing left: dorsal, lateral, ventral views, and close-up of multipored micropylar area, respectively. The thin ventral chorion on fig. 2 was torn during dissection. **5, 6.** Macrophotographs of same in ethanol, ventral and lateral views, respectively, showing glassy nature of chorion.

(roughly 10 times thicker than ventral chorion), when submerged in alcohol appearing glassy (figs. 5, 6), distinctly amber tinted, and clear, when critical-point dried, satiny tan above but frosted on border to attachment of ventral chorion; dorsal surface coarsely, seemingly irregularly nodular although nodules indistinctly arranged in linear rows on sides (fig. 2); earlier mature oocytes with nodules more closely set and sharply pointed and with less mass than those of later oocytes; ventral chorion mostly smooth, colorless, reflective under stereoscopic examination; under SEM examination dorsal chorion without surface sculpturing except for nodules, although early mature oocytes with

ridges between nodules; frosted area bordering ventral chorion pitted and with faint polygonal pattern; ventral chorion smooth.

MATERIAL STUDIED: Two females, Turkey: Erzurum: 22 km WSW Oltu, VI-23–2001 (J.G. Rozen); two females, same except VI-25–2001.

REMARKS: As is more fully explained with the respect to the oocytes of *Biastes brevicornis*, described below, the chorion of *Dioxys cincta* was in different stages of deposition on the mature oocytes within the same female. Compared with fully developed oocytes, earlier mature oocytes had a thinner dorsal chorion, from which the follicular tissue was more difficult to dissect.

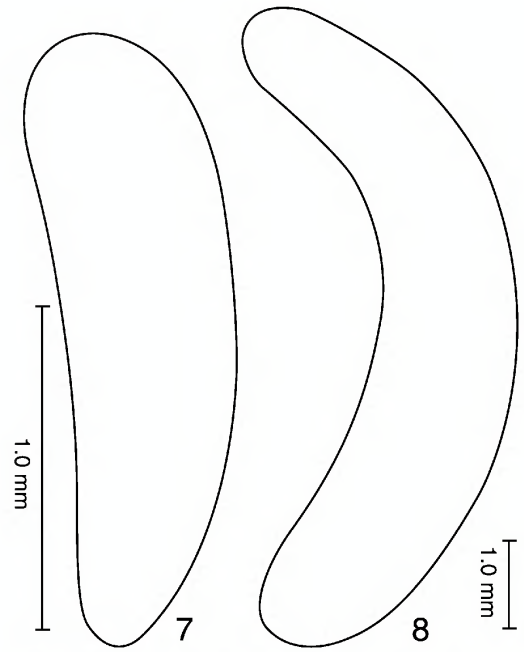
The thick, amber-tinted chorion provides the oocyte a dark border when seen from above or below (fig. 5), contrasting with the pale ovum. The amber chorion can easily be identified through the ovariole tissue before dissections.

Dioxys pacificus Cockerell

Because the mature oocyte of *Dioxys cincta* was so different from the egg of the North American *D. pomonae pomonae* Cockerell pictured and briefly described by Rozen and Favreau (1967: fig. 4), we examined the mature oocyte of another North American species, *D. pacificus*.

MATURE OOCYTE (fig. 7): Length 1.38–1.80 mm; maximum diameter 0.40–0.53 mm (N = 3); egg index 0.78 (medium). Shape symmetrical around moderately curved long axis; maximum width near anterior end; anterior end rounded; oocyte tapering posteriorly from maximum width; posterior end narrowly rounded; micropyle not evident under stereoscopic examination; under compound microscopic examination of inner surface of chorion, micropyle appearing as small circular area, presumably with numerous pores; area surrounding it with radiating lines extending outward in all directions 1.5–2.0 diameters of plate before fading. Chorion uniformly very thin, clear, smooth, reflective, and colorless.

MATERIAL STUDIED: Two females, Arizona: Cochise Co., 5 mi SW Apache, V-15–1988 (J.G. Rozen); one female, Arizona: Cochise Co., 4 mi E Willcox, V-8–1986 (J.G. Rozen); one female, Arizona: Cochise Co., 2 mi E Apache, V-9–1986 (J.G. Rozen).



Figs. 7, 8. **7.** Diagram of mature oocyte of *Dioxys pacificus*, lateral view, anterior end at top. **8.** Same of *Xylocopa* (*Proxylocopa*) *olivieri*. Figures drawn to different scales as indicated.

REMARKS: Because of the exceedingly thin and fragile nature of the chorion, we were unable to remove the follicular tissue from the anterior end of the mature oocytes of this species. However, we were able to find evidence of the micropylar area by removing the chorion with follicular tissue attached from the front end and examining it with a compound microscope.

The egg index (0.66) of *Dioxys p. pomonae*, given above, is based on the average of the two egg lengths (1.65 mm) provided by Rozen and Favreau (1967) divided by the average intertegular distance (2.51 mm) of 13 female specimens collected in association with that study, now preserved in the American Museum of Natural History.

The great differences in size and morphology of the mature oocytes/eggs between *Dioxys cincta* on the one hand and *D. p. pomonae* and *D. pacificus* on the other are unknown among other cleptoparasitic congeners and even within tribes. In their study of *D. p. pomonae*, Rozen and Favreau (1967:

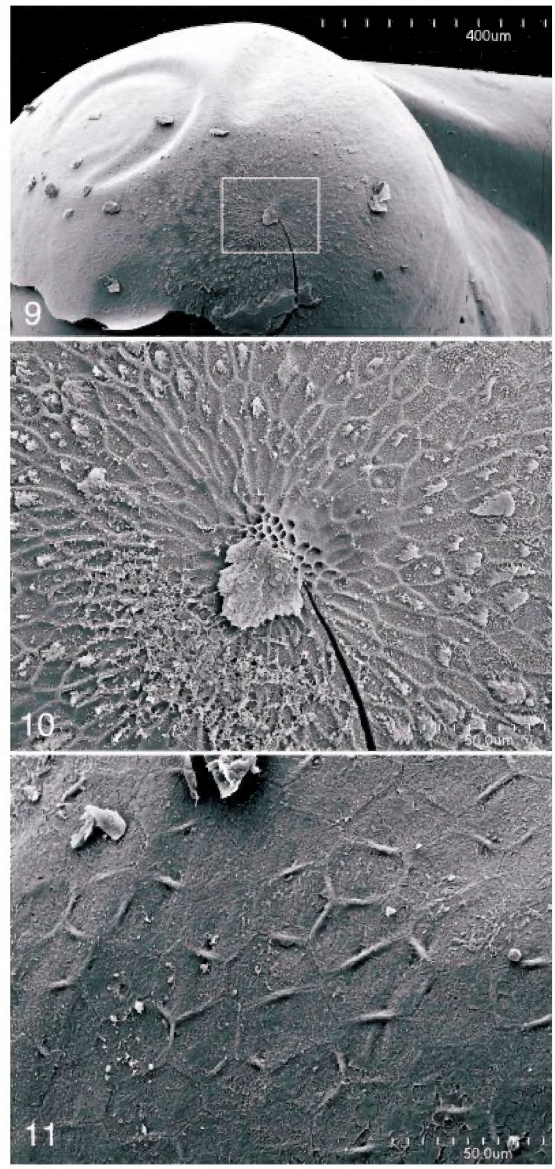
201) found "a small slit in the cell wall above the posterior end of the *Dioxys* egg apparently marking the spot through which the egg was inserted into the sealed cell." The assumption here was that the female cleptoparasite entered the nest of the ground-nesting host, which occupied short burrows, and penetrated the closed cell with her metasomal apex to lay an egg. The cell wall of the host bee was composed of masticated leaves. There is a tendency for cleptoparasitic bees that oviposit in sealed cells to have larger, relatively unmodified eggs (as do *D. p. pomonae* and *D. pacificus*) than do cleptoparasites that oviposit in cells that have yet to be sealed by host bees (to be discussed in greater detail by Rozen, in press). The females of *D. cincta* were collected while searching a vertical bank containing nests of a number of genera of osmiines, one or more of which were the hosts, but cell linings with masticated leaves were undetected. All cell walls were composed of hard soil, suggesting that the eggs of this species have to be deposited in cells that are still open. Might then the dwarf size of its mature oocytes and modified chorion be ways to escape detection by a returning host female?

APIDAE: XYLOCOPINAE: XYLOCOPINI

Xylocopa (*Proxylocopa*) *olivieri* Lepeletier

The shape (fig. 8) of the egg of *Xylocopa* (*Proxylocopa*) *olivieri* corresponds closely to published accounts of other members of the genus (Iwata, 1960, 1964, 1965).

MATURE OOCYTE (figs. 8–11): Length 7.2 mm; maximum diameter 1.7 mm; egg index 1.09 (nearly a giant). Shape elongate, approximately symmetrical around its moderately strongly curved long axis; anterior and posterior ends rounded; maximum diameter about three-quarters length from anterior end, surfaces tapering gradually beyond maximum diameter; micropyle not evident under stereomicroscopic examination but under SEM examination clearly multipored with numerous elongate polygons surrounding it (fig. 10), not unlike the anterior end of the egg of *Apis mellifera* Linnaeus (Erickson et al., 1986: 99). Chorion uniformly thin, smooth, transparent, colorless, reflective, lacking sculpturing and other ornamentation under stereoscopic examination; under SEM examination elongate polygonal pattern with raised borders distinct near anterior pole (fig. 10) but only faintly visible elsewhere (fig. 11).



Figs. 9–11. Mature oocyte of *Xylocopa* (*Proxylocopa*) *olivieri*. **9.** Anterior end. **10.** Close-up of micropylar area as identified in fig. 9 (micropyle partly obscured by follicular remnant). **11.** Faint polygonal pattern of mid oocyte.

MATERIAL STUDIED: One female, Turkey: Erzurum: 22 km WSW Oltu, VI-25–2001 (H. Özbek).

REMARKS: The egg size of the subgenus *Proxylocopa* was of interest because Alves-dos-Santos et al. (2002) hypothesized that gigantism in bee eggs (as defined by Iwata and Sakagami, 1966) may be an adaptation permitting the eggs and early instars to survive in nests in wood. They noted that most wood-nesting xylocopines had giant eggs, as do *Hylaeus* (Iwata and Sakagami, 1966) and *Tetrapedia*. They reasoned that such environments may be subject to loss of humidity and that large egg size might provide more water relative to surface area, thereby safeguarding from desiccation the developing embryo, which becomes a relatively large first instar. Since *X.* (*Proxylocopa*) is a xylocopine that has reverted to ground nesting, might its egg also have reverted to a smaller size approaching that of solitary, ground-nesting bees?

Although the egg index of this ground-nesting xylocopine is 1.09, technically "large", it is so close to the threshold (1.10) of a "giant" that it only questionably supports their hypothesis. Egg indices of other species of *Xylocopa* provided by Iwata and Sakagami (1966) ranged from 1.38 to 2.00; the range for all Xylocopinae was 1.21–2.00. Alternative explanations, of course, can be cited, namely, gigantism is now built into the genetics of the clade as a sort of evolutionary holdover, or a bank-nesting environment may be subject to unusual drying conditions not normally encountered in horizontal terrain. Other tests of this hypothesis might be the determination of egg indices of such wood-nesting taxa as *Anthophora* (*Clisodon*), *Centris* (*Xanthemisia*), and *C.* (*Heterocentris*) or almost any of the xeromelissines. Michener (1973) recorded the egg sizes of many allopines, but he used a index based on body length; those taxa might be worthy of reexamination

APIDAE: NOMADINAE: AMMOBATOIDINI

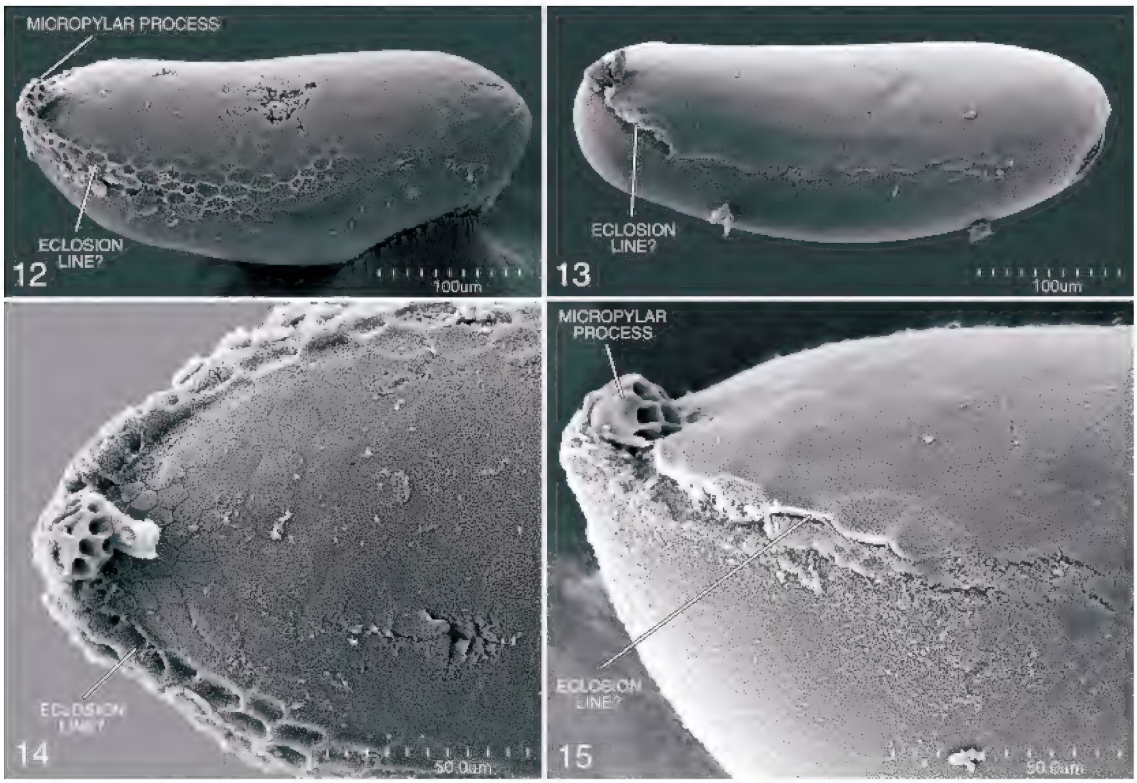
Mature oocytes/eggs of this tribe are known from *Ammobatoides abdominalis* (Eversmann) (Rozen, 2001) and the two species of *Holcopasites* described here. They are similar to one another in that they are wide relative to their length, have hook-shaped micropylar processes and a dorsal surface that is somewhat flattened, and exhibit a linear series of pits or fracturelike lines (tentatively called eclosion lines?) arising in front of or just below the micropylar processes and extending partway along the dorsolateral edge of the oocyte on both sides (figs.12, 13). The two species of *Holcopasites* have rounded front ends as seen in lateral view, with micropylar processes at the most anterior position. In contrast, the anterior end of the mature oocyte/egg of *A. abdominalis* is drawn out into a curved, sharp point that extends well beyond the micropylar process (Rozen, 2001: figs. 1, 2, 4, 5). The eclosion lines (?) of *H. insoletus* (Linsley) seem to be composed of placoid pits that become shallower posteriorly (figs. 12, 14) whereas those of *H. tegularis* (Hurd and Linsley) appear as fractures that skirt the polygonal edges of the dorsal surface (fig. 13, 15). However, more specimens need to be examined to confirm the consistency of this difference.

Holcopasites insoletus (Linsley)

MATURE OOCYTE (figs. 12, 14): Length 0.43–0.45 mm; maximum diameter 0.18–0.19 mm (N = 4); egg index 0.27 (dwarf). Incurved surface (presumably dorsal surface as judged by the egg/oocyte of *Ammobatoides abdominali*; Rozen, 2001) flat to gently curved; outcurved surface more strongly curved than incurved surface as seen from side; anterior end narrowing more gradually than posterior end as seen from side; greatest diameter somewhat posterior to midpoint as seen in lateral view; micropylar process hook-shaped (fig. 12). Chorion uniformly moderately thin, reflective, clear, glassy, very faintly amber when viewed stereoscopically in ethanol; when viewed by SEM, chorion dorsally with faint polygonal pattern; eclosion line (?) on each side consisting of deep polygonal pits at anterior end, becoming shallower posteriorly until they merge with general pattern (fig. 12).

MATERIAL STUDIED: One female, New Mexico: Hidalgo Co., Rodeo, VIII-28–2001 (J.G. Rozen, V. Giles).

REMARKS: Rozen (1965) diagrammed the egg insertion of an unidentified species of *Holcopasites*. Although the insertion position is correct, the egg itself is misleading in that it does not show the micropylar process at



Figs. 12–15. SEM micrographs of mature oocytes of *Holcopasites*, anterior end toward left. **12, 14.** *Holcopasites insoletus*, dorsolateral view of entire oocyte and dorsal view of anterior end, respectively. **13, 15.** *Holcopasites tegularis*, dorsolateral view of entire oocyte and of anterior end, respectively.

the anterior end and the egg shape is misleading, as judged by the shape of the mature oocytes of *H. insoletus* (fig. 12) and *H. tegularis* (fig. 13).

In his comparative study of the female reproductive systems of nomadine bees, Alexander (1996) also provided statistics concerning the egg index, number of mature oocytes, and ovarian formula of this species; his value for the egg index was 0.25 (dwarf).

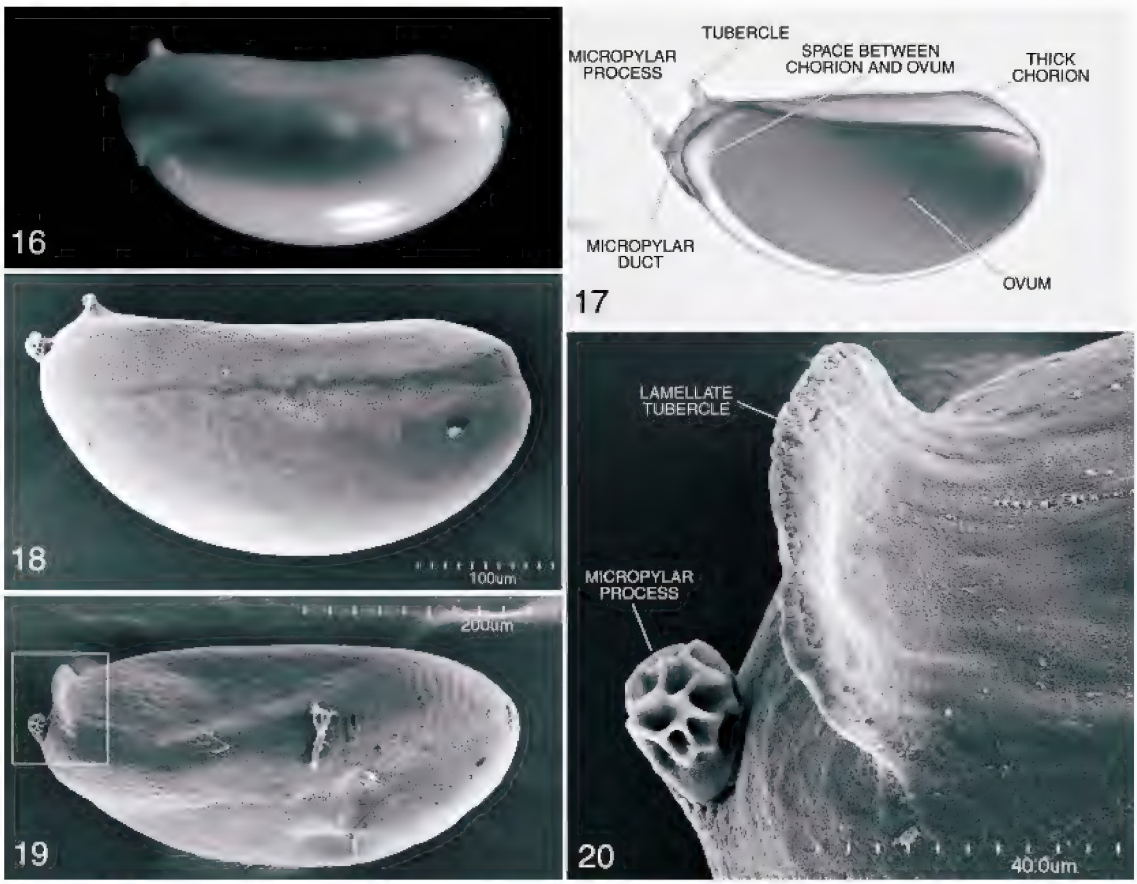
Holcopasites tegularis Hurd and Linsley

MATURE OOCYTE (figs. 13, 15): Length 0.44–0.48 mm; maximum diameter, lateral view 0.15–0.18 mm (N = 3); egg index 0.45 (dwarf). Shape as described for *Holcopasites insoletus* except posterior end more tapering than anterior end and widest part tending to be in front of midpoint; micropylar projection elevated about as far as its basal diameter, shorter than in *H. insoletus*. Chorion as described for *H. insoletus* except perhaps thinner and colorless; under SEM examination, dorsal surface smoother than lateral surface, which is faintly rough; eclosion lines (?) somewhat jagged, linear, following edge of dorsal polygonal placoids (fig. 15).

MATERIAL STUDIED: One female, Arizona: Cochise Co., 12 mi SW Apache, VIII-13–2001 (J.G. and B.L. Rozen).

APIDAE: NOMADINAE: BIASTINI

The egg of the biastine *Neopasites cressoni* (Crawford) was described by Torchio et al. (1967) and later compared with the egg/oocyte structure of *Rhopalolemma rotundiceps* Roig-Alsina in the same tribe (Rozen, et al., 1997). In these species and in *Biastes brevicornis* (Panzer), the micropylar apparatus appears as a dorsally projecting, hooklike process bearing numerous pores at the anterior end, very much as in the Ammobatoidini, at least some Nomadini (e.g., Iwata, 1960; Alexander and Rozen, 1987), probably the



Figs. 16–20. Mature oocytes of *Biastes brevicornis*, anterior end facing left. **16, 17.** Two lateral macrophotographs of entire oocyte, showing reflective, glassy nature of specimens in ethanol. **18–20.** SEM micrographs of entire oocyte, lateral and dorsolateral views, and close-up of anterior end of fig. 19, showing micropylar process and transverse tubercle, respectively.

Caenoprosopidini (Rozen and Roig-Alsina, 1991), and at least some Epeolini (Alexander and Rozen, 1987; Torchio and Burdick, 1988). Biastine eggs/oocytes, to the extent known, have one or more transverse tubercles on their dorsal surface, distinguishing them from the eggs/oocytes of all of these tribes. Within the tribe, *Rhopalolemma rotundiceps* is distinctive because of its more elongate egg shape compared with the other two exemplars and because its dorsal surface is covered with numerous transverse ridges, more distinct than those of *N. cressoni*. The dorsal surface of the mature oocyte of *B. brevicornis* is smooth except for the single conspicuous transverse tubercle near the front end, and therefore contrasts with oocytes of the other two genera.

Biastes brevicornis (Panzer)

The distinctive external shape of the egg of this species is the result of variation in the thickness of the chorion; the shape of the ovum, described below, is unremarkable.

MATURE OOCYTE (figs. 16–20): Length 0.47–0.50 mm; maximum width lateral view 0.19–0.25 mm, maximum width dorsal view 0.19–0.23 mm (see Remarks below); egg index 0.18 (dwarf). The following is based on mature oocytes with the chorion fully deposited, as discussed under Remarks: Shape bilaterally symmetrical; dorsal surface nearly flat to faintly concave behind transverse, thin, lamellate tubercle near anterior end (figs. 16–20); front end slightly swollen because of thick chorion, with micropylar pro-

cess arising anteriorly from swelling; posterior end broadly rounded in lateral view, broader than bulge at anterior end; maximum width as seen from side about midbody, as seen from above closer to front end than midbody; micropylar process elongate, bent dorsally so as to be hook-shaped, with numerous pores (fig. 20). Ovum (fig. 19) somewhat more than twice as long as maximum diameter, approximately symmetrical around its slightly curved long axis with its dorsal surface faintly incurved; maximum diameter near midpoint; ovum tapering anteriorly to rounded front end and posteriorly to more narrowly round rear end. Under stereoscopic examination in ethanol (fig. 16), chorion highly reflective, smooth (except for dorsal tubercle and micropylar process), colorless, and clear; that of dorsal surface glassy, very thick toward rear, becoming somewhat thinner anteriorly; after critical-point drying, chorion on dorsal surface appearing slightly yellowish, indistinctly pebbled on surface, sides and ventral surfaces smooth, highly reflective; under SEM examination (fig. 19), chorion dorsal surface with faint polygonal pattern over most of area; side and ventral surfaces with faint polygonal pattern (fig. 18).

Material Studied: One female, Turkey: Erzurum, Atatürk University Campus, VI-29–2001 (J.G. Rozen).

Remarks: In recent papers the term "mature oocyte" has referred to Iwata's (1955) category A and B oocytes (Alexander and Rozen, 1987) or to oocytes that have well-formed, thick chorions (e.g., Rozen, 2001). Most cleptoparasitic bees seem to have an unusually thick chorion, and this is especially true of the eggs of *Biastes brevicornis* (although it may generally be true for Nomadinae, as it is for *Dioxys cincta*, above). The mature oocytes recorded for this species are those with a detectable chorion and an evident micropylar process. However, we note a gradation in the development of the dorsal tubercle, the thickness of the dorsal chorionic surface, and the anterior chorionic bulge, with the later mature (lower in the ovarioles) oocytes having the chorion thicker in these areas, accounting for the variation in the dimensions. Earlier mature oocytes have smaller tubercles, even though the chorion elsewhere is evident and the ovum has reached its full size. Thus, there are degrees of maturity among those oocytes classified as mature oocytes. It follows that the amount of time required to deposit a thick chorion may be far greater than that for a thin-walled, nonparasitic bee egg. Of the 32 mature oocytes (table 1), that is, those with an evident chorion, 13 had a fully or nearly fully developed dorsal tubercle.

Egg placement of *Biastes brevicornis* in the host nest has not been observed. However, from the shape of the mature oocyte, it seems likely to be similar to egg placements of tribal relatives *Neopasites cressoni* (Torchio et al., 1967) and *Rhopalolemma rotundiceps* (Rozen et al., 1997); that is, the long axis of the egg parallel to the brood cell wall, the dorsal surface of the egg exposed to the cell lumen, and the remainder of the egg hidden in a groove in the cell wall.

Apidae: Nomadinae: Ammobatini

The mature oocytes of the Ammobatini show considerable morphological variation. All possess a more or less well-defined opercular area at the anterior end. This area may be flat, curved, or even slightly concave, and it may be variously ornamented with tubercles and patterns. depending on the taxon. The operculum may be surrounded by a flange (figs. 26, 41), which in most taxa is a single extended sheet of the chorion that, in a deposited egg, overrides the cell wall where the egg is inserted (Rozen, 1986b: fig. 6). In the mature oocyte, however, the flange hangs close to the body of the oocyte. The flange is broad in the case of *Sphecodopsis* (*Pseudodichroa*) or more limited as in the case of *Pasites maculatus* Jurine (fig. 44), *Parammobatodes rozeni* Schwarz (fig. 37), and "*Parammobatodes*" *orientana* (Warnke) (fig. 41). In *Oreopasites favreauae* Rozen (fig. 25), *O. barbarae* Rozen (fig. 32), and *O. linsleyi* Rozen (fig. 35), the flange is incomplete, represented only along the anterior edge and sides of the operculum but not in the rear. The flange is totally missing in *O. vanduzeei* Cockerell (fig. 30) (as it may be in *Ammobates carinatus* Morawitz), but is replaced with a thick opercular rim. All taxa examined except for the two species of *Sphe-*

codopsis (*Pseudodichroa*) exhibit dorsal transverse folds of the chorion toward the posterior end, a feature apparently unique to this group of cleptoparasitic bees. These folds allow the egg to be bent back on itself at the time of deposition. Oocytes of *Pas. maculatus* (fig. 47), *Par. rozeni* (fig. 38), and "*Par.*" *orientana* (fig. 43) possess micropyles consisting of a single pore; micropyles of other tribal members are multipored. The mature oocytes of *Pas. maculatus* and the "*Par.*" *orientana* can obviously be distinguished on the basis of their different sizes, but they are quite similar in shape and structure. Opercular tubercles of *Pas. maculatus* (fig. 45) are larger than those of "*Par.*" *orientana* (which in fig. 42 are scarcely discernible), although the extent of expression of these tubercles appears to be subject to variation in size from one oocyte to the next in some taxa. The polygonal opercular pattern of the latter (fig. 42) seems to contrast with the unpatterned opercular surface of *Pas. maculatus* (fig. 45) under SEM examination. The huge, strongly tuberculate, amber operculum of *A. carinatus* (fig. 21) distinguishes this species from all others treated here, as does the flat ebony-colored operculum of *Par. rozeni* (figs. 36, 37).

Ammobates carinatus Morawitz

The mature oocyte of this species was illustrated and briefly described by Alexander and Rozen (1987). It is redescribed here to add additional details from SEM examination, using the female dissected for the previous study.

MATURE OOCYTE (figs. 21–24): Length 1.2 mm; maximum diameter behind operculum 0.28 mm (N = 1); egg index 0.47 mm (dwarf) (as reported by Alexander and Rozen, 1987). Opercular area large compared with rest of oocyte, its surface curved and bearing variable number of projecting tubercles near anterior margin; some of these tubercles flattened, others slightly capitate (fig. 23); sides of opercular area possibly representing flange of most other ammobatines; behind operculum, oocyte approximately symmetrical around its nearly straight long axis, tapering to round posterior end, its dorsal surface with numerous transverse folds (fig. 21); micropyle consisting of a number of small, closely grouped pores apparently on a low mound close to the anterior edge of operculum (fig. 24). Chorion of operculum conspicuously amber tinted in ethanol, with faint polygonal pattern in some areas under SEM examination; chorion of remainder of oocyte clear, smooth, colorless.

MATERIAL STUDIED: One female, Morocco: 10 km S Skirhate nr. Rabat, IV-29–1968 (J.G. Rozen, E. Suissa).

REMARKS: See Remarks under *Pasites maculatus*, below.

Oreopasites (*Oreopasites*) *favreauae* Rozen

The following description is based on the same material used by Alexander and Rozen (1987) in their study of the egg index and numbers of ovarioles and mature oocytes of this species (then cited as *Oreopasites* sp. A).

MATURE OOCYTE (figs. 25–27): Length 0.65 mm; maximum diameter 0.20 mm (N = 1); egg index 0.49 as indicated by Alexander and Rozen (1987) (dwarf). Operculum with narrow flange only along front and sides (fig. 25); opercular surface about as wide as long, with numerous uneven rounded tubercles that do not invade area behind operculum (fig. 25); dorsal surface behind operculum convex in lateral view, with numerous transverse folds dorsally (as in fig. 28); micropyle a small cluster of pores on slightly raised area near anterior margin of operculum (fig. 26). Chorion of operculum with scattered tubercles and uneven surface (figs. 25, 26); chorion elsewhere smooth, thin, colorless, except ventral chorion nodular with nodules variably expressed and larger (fig. 27) than those of *Oreopasites vanduzeei* (fig. 29).

MATERIAL STUDIED: Two females, Arizona: Cochise Co., 4 mi E Willcox, IX-5–1986 (J.G. and B.L. Rozen).

Oreopasites (*Oreopasites*) *vanduzeei* Cockerell

The mature oocyte of this species was previously described and illustrated by Rozen (1986a), but the egg index was not calculated and additional details concerning the operculum can now be provided.

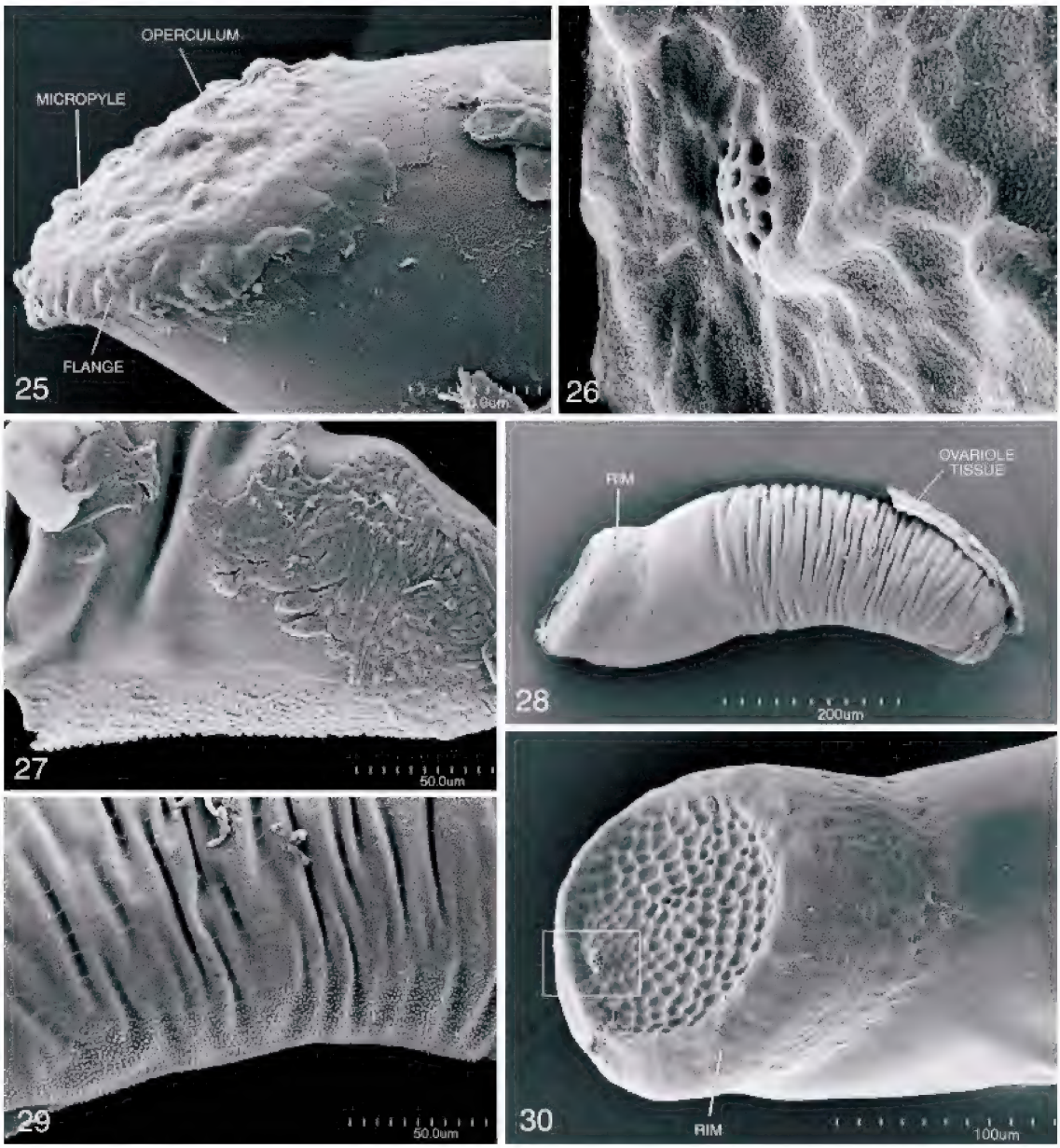
MATURE OOCYTE (figs. 28–31): Length

Figs. 21–24. SEM micrographs of mature oocytes of *Ammobates carinatus*, anterior end facing left. **21.** Entire oocyte, lateral view. **22.** Operculum, top view, showing position (white rectangle) of micropyle. **23.** Close-up of anterior part of operculum showing forms of tubercles, lateral view. **24.** Close-up of micropyle as identified in fig. 23.

0.68 mm; maximum diameter 0.18–0.20 mm (N = 4); egg index 0.35 (dwarf). Opercular surface slightly concave (fig. 30) (not convex as suggest by Rozen, 1986a: fig. 1), surrounded by complete, thick, circular rim, without flange; oocyte immediately behind operculum (fig. 28) slightly curving dorsally and then immediately curving downward so that dorsal surface outcurved, with fine annulations expressed both dorsally and ventrally, as seen in lateral view; rear somewhat narrowly rounded; micropyle small, multipored area just inside of rim at anterior edge of operculum (fig. 31). Chorion under stereoscopic examination clear, faintly amber, on operculum, glassy; under SEM examination, opercular chorion with raised polygonal boundaries giving surface within rim uniform, shallowly pitted pattern (fig. 30); rim with faint polygonal pattern (fig. 30); chorion elsewhere with faint lines here and there, otherwise smooth except posterior ventral surface nodular, with nodules finer and more evenly spaced (fig. 29) than those of *O. favreauae* (fig. 27).

MATERIAL STUDIED: Two females, Arizona: Cochise Co., 2 mi E Apache, IV-30–1993 (J.G. Rozen).

REMARKS: The ovaries of one of the females contained the chorions of numerous reabsorbed oocytes, as noticed for a female of *Parammobatodes rozeni*, below. These chorions had accumulated in the lower ends of the ovarioles, often clinging to the sides of viable mature oocytes. The most durable part of the depleted oocytes was the pitted operculum. Whereas there were 15 mature oocytes, reabsorbed mature oocytes num-

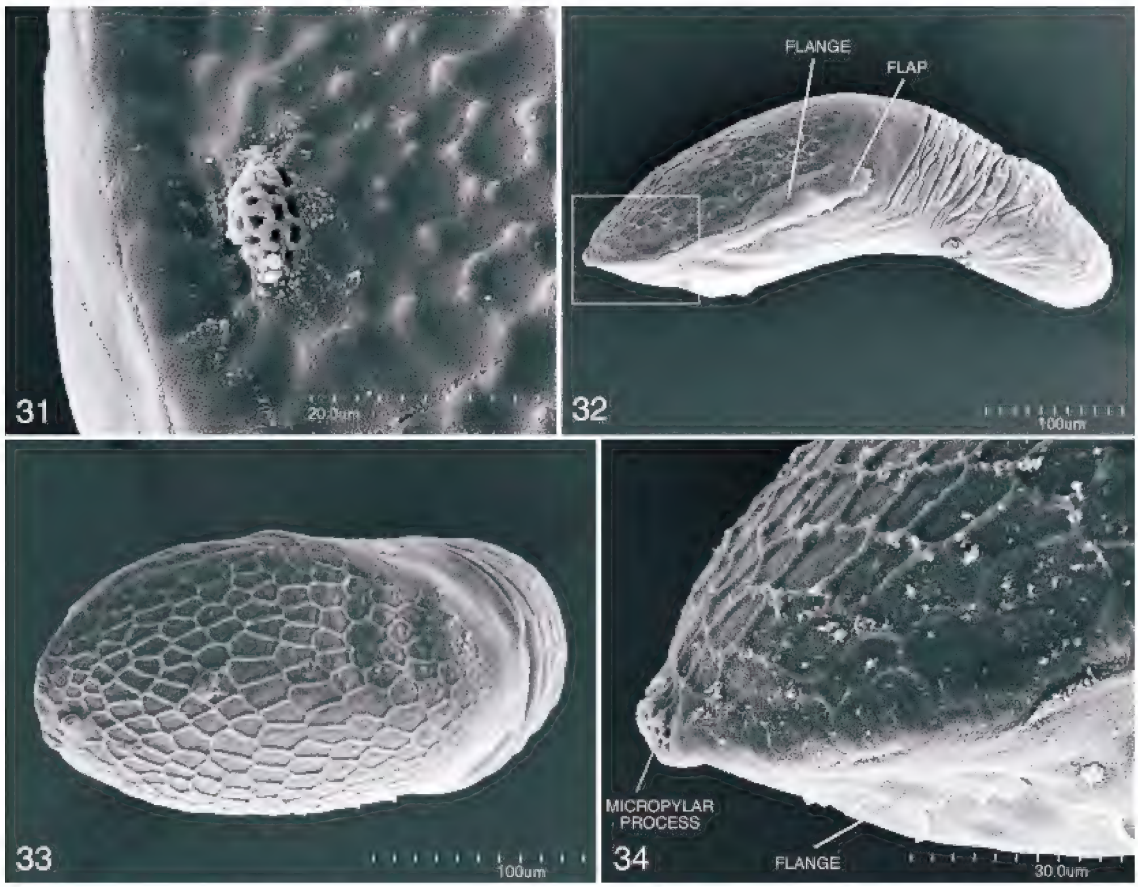


Figs. 25–30. **25–27.** SEM micrographs of mature oocytes of *Oreopasites favreauae*, anterior ends toward left. **25.** Anterior end of oocyte, lateral view. **26.** Micropylar area of another oocyte, dorsal view. **27.** Posterior end of oocyte, lateral view, showing nodular ventral area. **28–30.** SEM micrographs of mature oocytes of *Oreopasites vanduzeei*, anterior ends toward the left. **28.** Entire oocyte, lateral view, with part of ovariole tissue clinging dorsally. **29.** Near posterior end of oocyte, showing fine nodules ventrally contrasting with fig. 27, both to same scale. **30.** Anterior end of oocyte, showing lack of flange; micropyle in rectangle.

bered 28. In neither the specimen of *Parammobatodes rozeni* nor of *Oreopasites vanduzeei* did we encounter an oocyte that was only partly reabsorbed, suggesting, perhaps, that reabsorption is a quick process.

Oreopasites (*Perditopasites*) *barbarae* Rozen

MATURE OOCYTE (figs. 32–34): Length 0.40–0.46 mm; maximum width 0.14–0.16



Figs. 31–34. **31.** SEM micrograph of micropylar area of oocyte of *Oreopasites vanduzeei* outlined in fig. 30. **32–34.** SEM micrographs of mature oocytes of *Oreopasites barbarae*, anterior ends facing left. **32.** Entire oocyte, lateral view. **33.** Anterior part of oocyte, maximum profile, dorsal view. **34.** Close-up of anterior end of oocyte outlined by rectangle in fig. 32.

mm (dorsal width about 0.01 mm greater than lateral width) (N = 9); egg index 0.63 (small). Opercular surface curved, seemingly a continuum with dorsal surface behind it (for alternative interpretation of morphology, see Remarks below), so that dorsal surface of anterior part of oocyte slightly flattened, broader dorsally than laterally; flange so short as to be clearly visible only with SEM, extending along anterior margin of oocyte and clinging to ventral surface and lateral surfaces, as seen in lateral view; flange posteriorly ending in flap (fig. 32); remainder of oocyte shaped about like that of *Oreopasites linsleyi* (fig. 35); micropyle multipored, at anterior edge of operculum (fig. 34). Chorion clear, colorless; under SEM examination dorsal chorion with polygonal pattern with raised borders from front edge running posteriorly to about twice dorsal width of oocyte (fig. 33); ventral surface smooth, without nodules as found in *O. favreauae* and *O. vanduzeei*.

MATERIAL STUDIED: Two females, Arizona: Cochise Co., 13 mi SW Apache, VIII-31–1988 (J.G. Rozen).

REMARKS: Several interpretations of the morphology of the mature oocyte of this species (and of that of *Oreopasites* (*Perditopasites*) *linsleyi*) come to mind. The first, expressed in the description above, is that the posterior boundary of the operculum is lost so that the opercular surface simply grades into the surface behind it, as suggested by the loss of the posterior part of the flange in *Oreopasites favreauae* (fig. 25) and *O. van-*

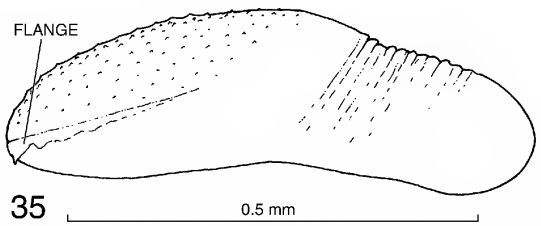


Fig. 35. Diagram of mature oocyte of *Oreopasites linsleyi*, lateral view, anterior end facing left.

duzeei (fig. 30), even though the opercula of these two taxa are identifiable as being nearly circular. Another interpretation of the anatomy of the mature oocytes of the two species of the subgenus *Perditopasites*, we think equally supported, is that the operculum has become greatly elongate, so that it is twice as long as wide and its entire surface is expressed by the polygon pattern. The latter explanation is supported, at least in the case of *O. barbarae*, by the long lateral extension of the flange, which seems to reach for the posterior boundary of the polygonal surface, as seen in figure 32.

Oreopasites (*Perditopasites*) *linsleyi* Rozen

Because it was impossible to dissect oocytes of this species intact, the following description and figure 35 are based on fragments, leaving certain details obscure.

MATURE OOCYTE (fig.35): Length 0.55–0.63 mm; maximum diameter 0.18 mm; egg index 0.60 (small). Opercular surface curved, with narrow flange anteriorly, but flange disappearing posteriorly so that posterior opercular edge not defined, at least under stereoscopic and compound microscope examination; as seen in lateral view (fig. 35), opercular surface a continuum with dorsal surface of oocytes (but see Remarks under *O. barbarae*, above); posterior part of oocyte with numerous, well-defined, transverse folds dorsally, these folds not reaching ventral surface; micropyle a median cluster of pores close to anterior edge of operculum, not on projection. Chorion clear, unpigmented; chorion of operculum and anterior dorsal surface thicker than elsewhere, with polygon pattern of fine ridges when viewed stereoscopically or by compound microscope; unlike in *Oreopasites barbarae*, intersections of ridges more elevated, giving surface rather uniform, finely nodular appearance; elsewhere chorion smooth, reflective, apparently without sculpturing; chorion not studied by SEM.

MATERIAL STUDIED: One female, New Mexico, Hidalgo Co., 5 mi N Rodeo, IX-1–1989 (J.G. and B.L. Rozen, and R.L. Foster).

REMARKS: We note that the largest oocytes of three of the four species of *Oreopasites* described here are nearly equal in length, with *O. barbarae* being the exception. As a result, the egg indices of these three vary considerably in relation to female body size: *O. vanduzeei* is by far the largest species (egg index 0.36), *O. favreauae* the next largest (egg index 0.49), and *O. linsleyi* the shortest and most slender (egg index 0.60). Although *O. barbarae* is much smaller than *O. linsleyi*, its egg index (0.63) is somewhat larger than that of the others.

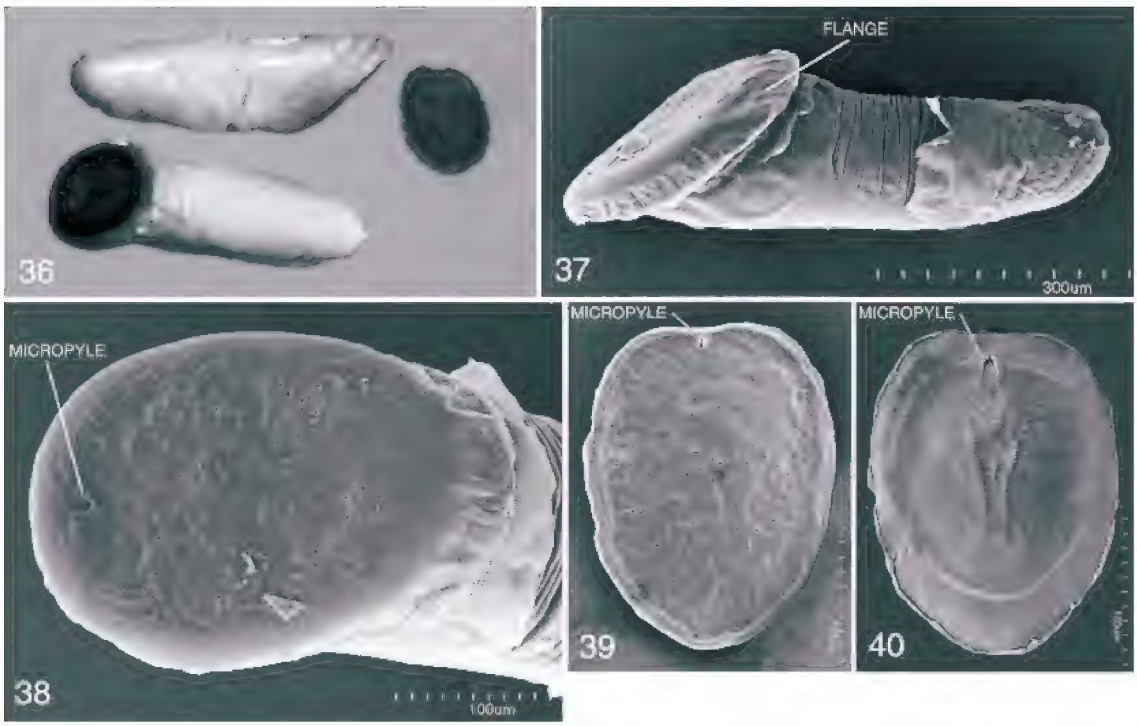
Parammobatodes rozeni Schwarz

The description of this new species is appended to this paper.

MATURE OOCYTE (figs. 36–40): Length 0.73–0.75 mm; maximum diameter behind operculum 0.20–0.23 mm (N = 5); egg index 0.41 (dwarf). Operculum flat, its surface with very small tubercles, appearing merely uneven through stereomicroscope; behind operculum, dorsal surface nearly straight to slightly concave in lateral view, with numerous transverse folds (fig. 37); ventral surface more curved; micropyle a single pore close to anterior edge of operculum (figs. 38, 39), penetrating obliquely to open as single pore on inner surface (fig. 40). Chorion of operculum translucent, ebony with amber tints in ethanol or dry (fig. 36); that of flange and rest of oocyte untinted, clear (fig. 36); under SEM, chorion of operculum with faint but distinct polygonal pattern externally (figs. 38, 39); internally this pattern absent (fig. 40).

MATERIAL STUDIED: One female, Israel: S Negev, 15 km N Shizzafon Jct. V-9–1997 (J.G. and B.L. Rozen).

REMARKS: A noteworthy feature of the ovaries of this specimen was that five flat ebony opercula (fig. 36), with totally deplet-



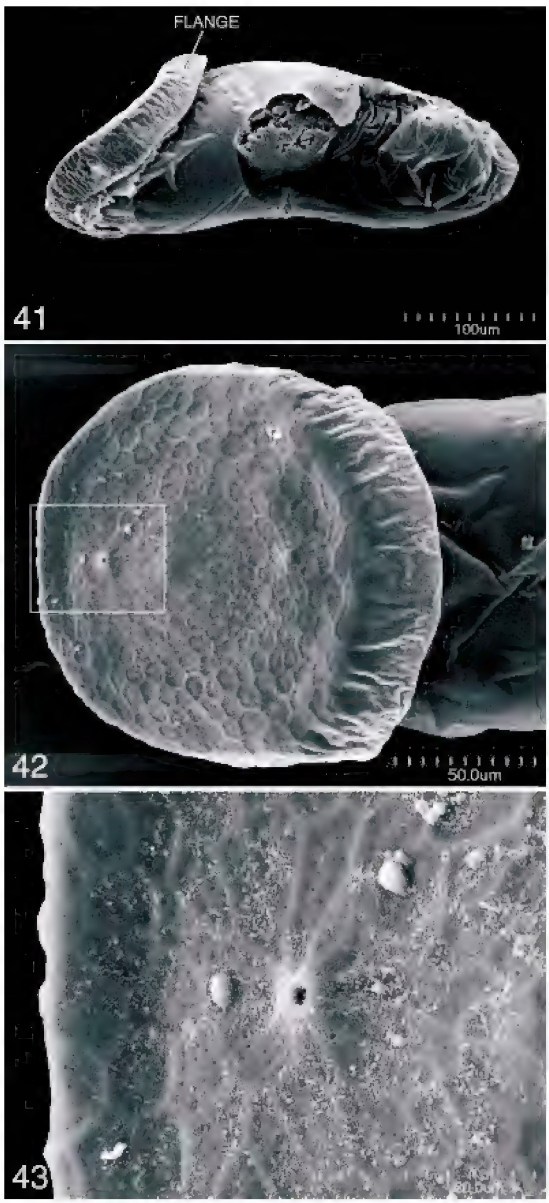
Figs. 36–40. Mature oocytes of *Parammobatodes rozeni*. **36.** Macrophotograph of two oocytes, various views, and operculum of reabsorbed oocyte. **37.** SEM micrograph of entire oocyte, lateral view, anterior end facing left. Much of midchorion torn away revealing transverse folds of ovum. **38.** SEM micrograph of operculum, maximum outline, showing micropyle with single pore near anterior margin. **39, 40.** SEM micrographs of opercula of reabsorbed oocytes, exterior and interior views, respectively, anterior ends toward top of page.

ed chorions attached in most cases, were lodged near the calyx of the left ovary and six near the calyx of the right ovary. Some were found singly, others closely stacked against one another by twos and threes. We interpret these oocytes to be reabsorbed, a feature we also noticed in only one specimen of *Oreopasites vanduzeei*, of all specimens dissected in this study. These oocytes indicate that reabsorption occurs after the oocyte is fully mature, with the chorion completely pigmented in all cases. Their presence suggests that the female may have been unable to find host nests with cells in the right state for oviposition. The dark, ebony color of the operculum itself is a unique feature, not found in any other species whose oocytes have been examined by the authors. It is far darker than the amber hue of the mature oocyte of *Ammobates carinatus* and is restricted to the operculum and not to the flange, which is colorless. Earlier mature oocytes have less coloring of their opercula than do later oocytes. Because of the dark color of the opercula, mature oocytes were easily detected through the follicular tissue of the ovariole even without dissection.

"*Parammobatodes*" *orientana* (Warnke)

This species was originally described by K. Warnke as *Pasites* (*Parammobatodes*) *orientanus*. Its generic name here is placed in quotes because the species is thought to belong to a new genus, yet to be named, species of which attack the nests of *Nomioides*, as mentioned by Michener (2000: 643). Females of this species were entering burrows of *N. minutissimus* (Rossi), kindly identified by Yuriy A. Pesenko.

MATURE OOCYTE (figs. 41–43): Length 0.48–0.50 mm; maximum diameter 0.16–



Figs. 41–43. SEM micrographs of mature oocyte s of "*Parammobatodes*" *orientana*, anterior ends facing left. **41.** Entire oocyte, lateral view. **42.** Operculum, dorsal view. **43.** Close-up of micropylar area identified by rectangle in fig. 42.

0.19 mm; egg index 0.52 (small). Shape as described for *Pasites maculatus*; micropyle a single median pore near anterior edge of operculum (figs. 42, 43), similar to that of *P. maculatus* except on slight mound. Chorion clear, untinted, appearing thinner and less sclerotized than that of *P. maculatus*, with several indistinct tubercles; under SEM examination, opercular surface (figs. 42–43) with distinct polygonal pattern with fine pits scattered within each polygon; chorion elsewhere smooth.

MATERIAL STUDIED: Two females, Turkey: Erzurum, Atatürk University Campus, VI-29–2001 (J.G. Rozen).

REMARKS: See Remarks under *Pasites maculatus*, below.

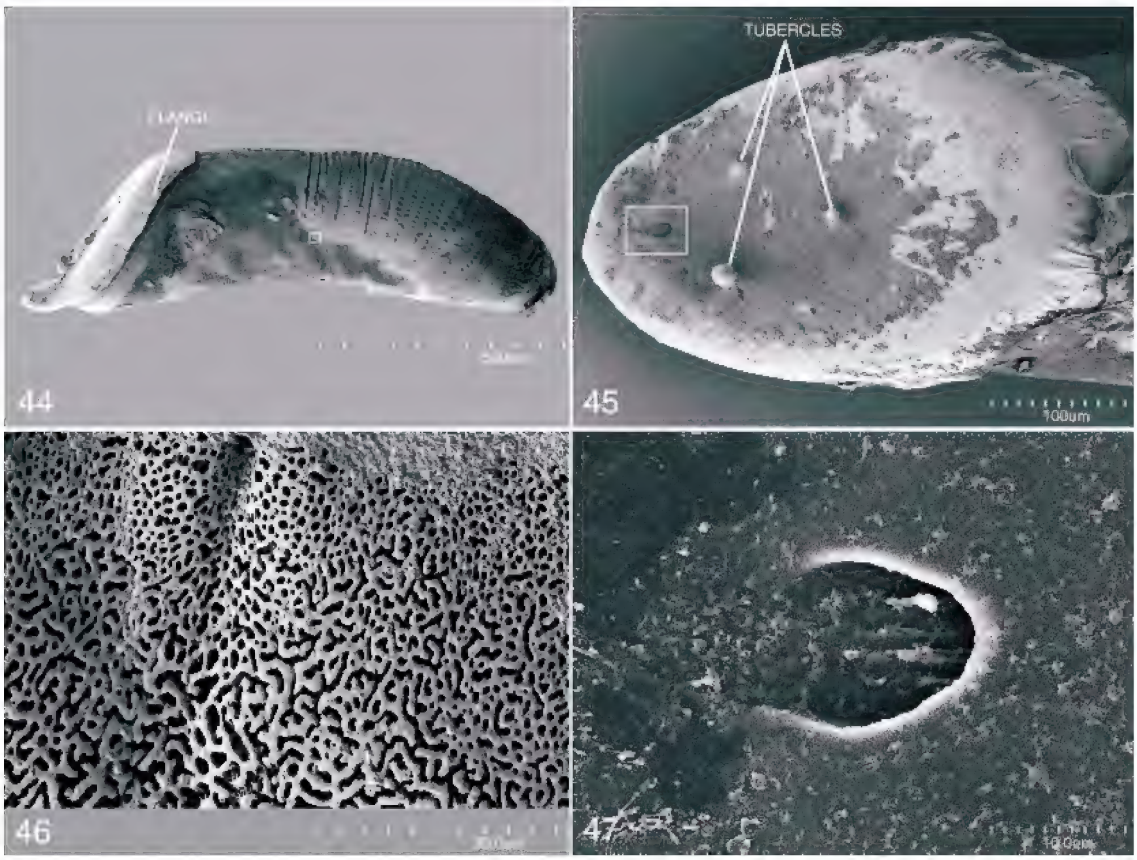
Pasites maculatus Jurine

Rozen (1986b) described the oviposition habits and egg of this species based on observations and collections from Pakistan.

MATURE OOCYTE (figs. 44–47): Length 1.20–1.35 mm (N = 11); maximum diameter immediately behind operculum 0.35 mm; egg index 0.47 (dwarf). Operculum oval, longer than broad (fig. 45); flange surrounding entire operculum, turned down over oocyte, not in same plane as operculum (fig. 44); opercular surface usually with 3 or 4 rounded tubercles (fig. 45), but these tubercles varying in size from one oocyte to another and sometimes not visible; oocyte approximately symmetrical around its gently down-curving long axis (outcurved surface dorsal), tapering to narrowly round posterior end, its dorsal surface with numerous transverse folds (fig. 44); micropyle a simple median pore with duct through chorion at anterior end of operculum (figs. 45, 47). Chorion clear, smooth except for opercular tubercles, untinted (operculum tinted, presumably by dye from the label ink, as a result of preservation) seen through stereomicroscope; that of operculum thicker than elsewhere; by SEM examination, chorion of operculum without polygonal pattern (but see Rozen [1986b: fig. 5] for the opercular surface of egg of same species from Pakistan); chorion of rest of oocyte under SEM examination smooth where covering transverse folds, but extensive area anterior to folds and ventrally finely pitted, fibrous, lacelike, as seen in figure 46.

MATERIAL STUDIED: One female, Turkey: Erzurum, Atatürk University Campus, VII-10–2001 (J.G. Rozen) at nest entrance of *Pseudapis*.

REMARKS: Oocytes whose chorion, especial-



Figs. 44–47. SEM micrographs of mature oocyte of *Pasites maculatus*, anterior end facing left. **44.** Entire oocyte, lateral view. **45.** Operculum, maximum profile, with micropylar area identified by rectangle. **46.** Chorionic ornamentation from area of oocyte identified by rectangle in fig. 44. **47.** Micropyle with single pore from area identified by rectangle in fig. 45.

ly the flange (Rozen, 1986b), was visible through the follicular tissue were considered mature. The variation in size of the opercular tubercles did not appear to be a function of the maturity of the oocytes since a mature oocyte without tubercles was the lowest in its ovary.

The transversely folded dorsal chorionic surface of the oocyte has also been noted for *Oreopasites vanduzeei* (Rozen, 1986a: fig. 1), *O. linsleyi* (above), *Ammobates carinatus* (Alexander and Rozen, 1987: fig. 4), and "*Parammobatodes*" *orientana*, above. Thus, five members of the Ammobatini share this unique feature, which no doubt signifies that each bends its egg into a "U" when ovipositing (see Rozen, 1986b: fig. 6). Interestingly, both species of *Sphecodopsis* (*Pseudodichroa*), in the same tribe, do not bend their eggs (Rozen and Michener, 1968: figs. 8–12).

The ovarian formula, whether 4:4 or 4:5, for *Pasites maculatus* and 4:4 for "*Parammobatodes*" *orientana*, below, is unusual for the Nomadinae, which tend to have more ovarioles than 4 per ovary, the plesiomorphic number for the Apidae (Alexander, 1996; Michener, 2000; Rozen, in press).

Sphecodopsis (*Pseudodichroa*) *capensis* (Friese)

The egg of this species and the following one were described and illustrated by Rozen and Michener (1968). The egg index of 0.72 (table 1) categorizes it as small. The index

was calculated by taking the median value (1.65 mm) of the range of egg lengths given by Rozen and Michener (1968: table 2) and dividing it by the mean intertegular distance (2.30 mm) of the seven females associated with their study and housed in the American Museum of Natural History.

MATERIAL STUDIED: Two eggs, Republic of South Africa: Cape of Good Hope Peninsula, Kommetjie, X-29–XI- 9–1966 (J.G. Rozen, C. D. Michener) from nests of *Scrapter longula* (Friese).

Sphecodopsis (*Pseudodichroa*) *fumipennis* (Bischoff)

The egg index of 0.67 (table 1) of this species categorizes the egg as small. The index was calculated by taking the median value (1.95 mm) of the range of egg lengths given by Rozen and Michener (1968) and dividing it by the mean intertegular distance (2.95 mm) of the three females associated with their study housed in the American Museum of Natural History. Because they described the egg in some detail, it is not redescribed here, except to add that the incurved surface is dorsal. However, SEM examination of two eggs (figs. 48–51) shows the strong polygonal pattern of raised borders that seems responsible for the rigidity of the chorion (fig. 48), and the multipored micropyle (fig. 51) was revealed near the anterior edge of the smooth opercular flap of an egg that had apparently eclosed.

MATERIAL STUDIED: Two eggs, Republic of South Africa: Cape of Good Hope Peninsula, Kommetjie, X-29–XI- 9–1966 (J.G. Rozen, C.D. Michener) from nests of *Scrapter crassula* Cockerell.

APIDAE: APINAE: MELECTINI

Eggs/oocytes of the following melectine taxa have been described and/or illustrated: *Thyreus japonicus* Friese (Iwata, 1955), *T. lieftincki* Rozen (Rozen, 1969), *Zacosmia maculata* (Cresson) (Torchio and Youssef, 1968), and *Xeromelecta californica* (Cresson) (Torchio and Trostle, 1986). We describe here the mature oocytes/eggs of *Melecta* and *Thyreomelecta kirghisia* and provide additional information on *T. lieftincki* and *X. californica*. So far as known, eggs of all melectines are elongate, curved, and either parallel-sided or tapering gradually from the anterior end toward the posterior end, with the front end somewhat more broadly rounded than the posterior end (e.g., figs. 52, 53). Most appear dull and somewhat opaque whether in alcohol or dry, and none have chorionic ornamentation beyond the dull chorion as seen under stereoscopic examination. The differences between them by SEM examination seem slight, involving microstructure of the chorion (compare fig. 56 with fig. 59).

Melecta albifrons albovaria Erichson

MATURE OOCYTE (figs. 52, 54, 55): Length 2.80–3.35 mm; maximum diameter 0.55–0.65 mm; egg index 0.59 (small). Shape (fig. 52) elongate, approximately symmetrical around moderately curved long axis; anterior end broadly rounded; middle part nearly parallel-sided, gradually tapering in posterior quarter; posterior end rounded; micropyle not evident under stereoscopic examination; under SEM examination, micropyle not viewed but area around it with elongate polygons directed toward it, these polygons with incised borders. Chorion under stereoscopic examination smooth, semi-opaque, dull, very thin, and lacking sculpturing and other ornamentation; under SEM examination, surface of at least most of chorion covered with faint polygonal pattern (fig. 55) except this pattern more evident at anterior pole (fig. 54); under high magnification, chorion carpeted with truncated fibrous projections (much as in figs. 58, 64); at extreme posterior end of oocyte (not visible in fig. 55), polygonal pattern not evident and projections becoming more elongate and less truncated (much as in figs. 63, 65).

MATERIAL STUDIED: Two females, Turkey: Erzurum: 22 km WSW Oltu, VII-02–2001 (J.G. Rozen) flying in front of vertical bank; one female, same except VI-23–2001.

REMARKS: Michael S. Engel, University of Kansas, kindly identified the adults of this species.

The follicular tissue was difficult to remove from the oocytes of this species and all other melectines examined in this study. For this reason, we were unable to examine the

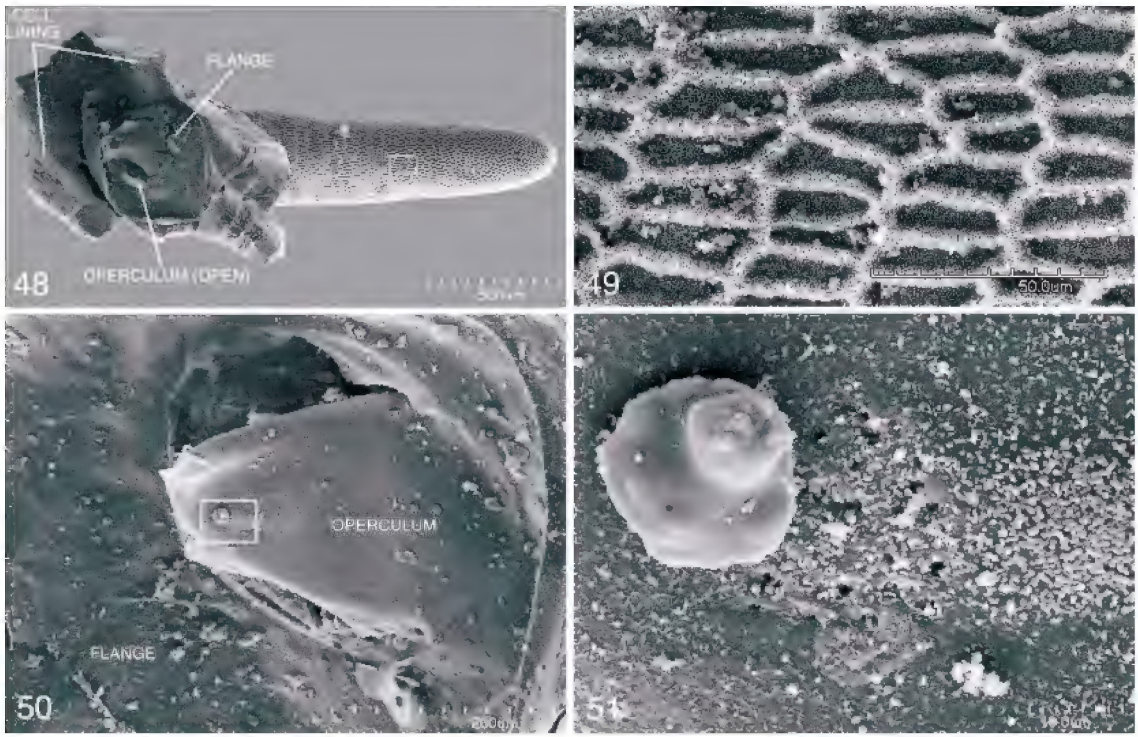


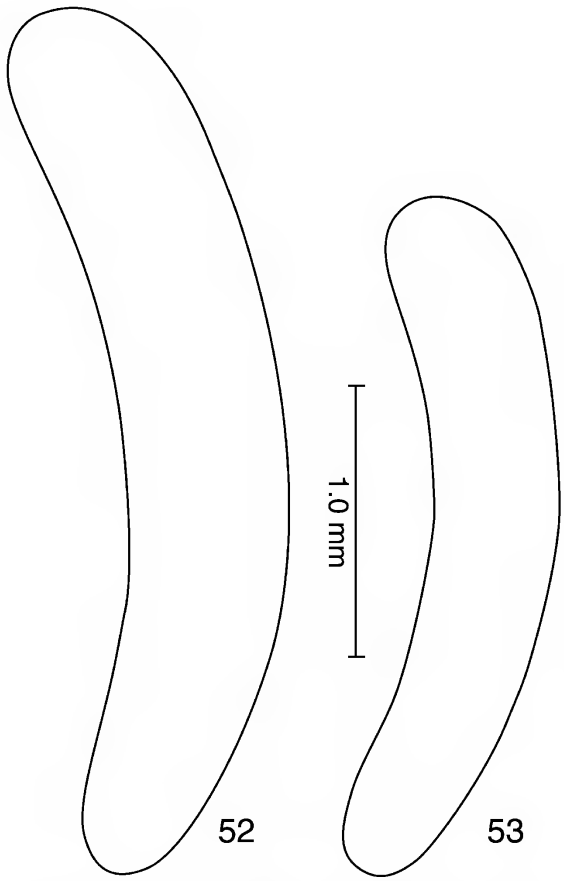
Fig. 48–51. SEM micrographs of eggs of *Sphecodopsis* (*Pseudodichroa*) *fumipennis*, anterior ends facing left. **48.** Entire egg, dorsal view, with partial cell lining of host, *Scrapter crassula* Cockerell, attached at anterior end. **49.** Close-up of chorion from area identified by rectangle in fig. 48. **50.** Opened operculum of another egg, dorsal view, showing position of multipored micropyle (rectangle). **51.** Close-up of micropyle in fig. 50.

micropylar region of *Melecta albifrons albovaria*. The change in chorionic microstructure at the extreme posterior end may somehow relate to the mechanism of attachment of the egg to the cell closure.

Melecta species

The egg (described below) of an unknown species of *Melecta* was found attached by its posterior end to the cell closure of *Anthophora* (*Lophanthophora*) nr. *fulvitarsis* Brullé (kindly identified by Robert W. Brooks, University of Kansas). The long axis of the cell was vertical, and the egg hung straight down from the smooth inner surface of the closure. Although the lower part of the cell had been destroyed during our excavation, the cell closure and the upper part remained. We immediately noticed two conspicuous holes on the inner surface of the closure, the closest to the egg being 3 mm away (figs. 60, 61). Each hole was about 1 mm in diameter and was filled with a rough mass of soil that extended beyond the inner surface of the closure. Later, another egg (or egg chorion) was seen imbedded in the dried provisions clinging to the sidewall; this had either hatched, been dropped onto the provisions when deposited, or been dislodged from the closure during our excavation. Thus two eggs, presumably from different females (otherwise, why two holes?), had been introduced into the closed cell.

Hence, the oviposition behavior of this species appears almost identical to that described for *Melecta separata callura* (Cockerell) by Thorp (1969) and for *M. pacifica* Cresson by Bohart (1970). Malyshev's (1928: fig. 7) photograph of the egg of *Melecta armata* Panzer attached to the cell closure of *Anthophora acervorum* Linnaeus is consistent with these accounts. Torchio and



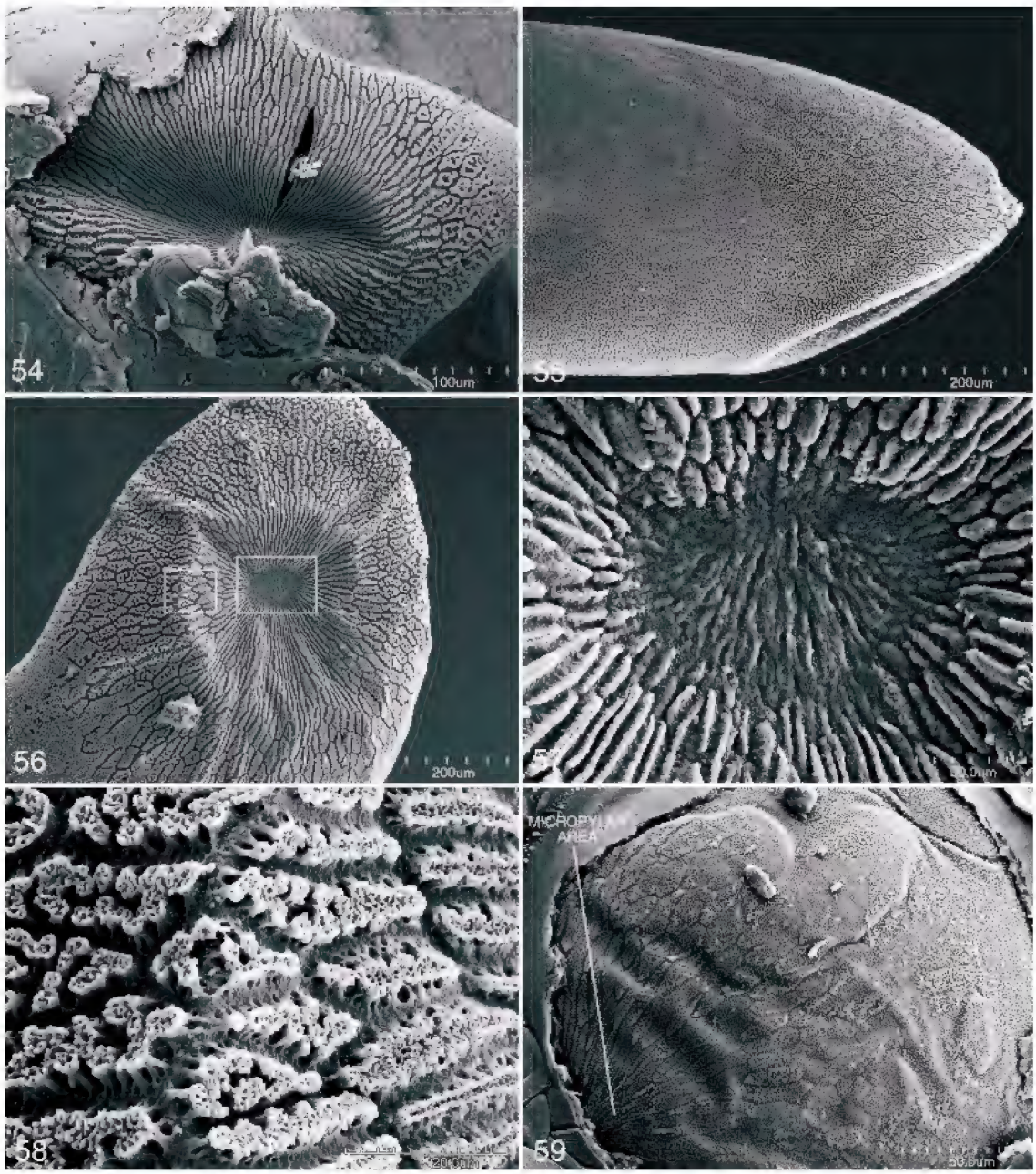
Figs. 52, 53. Diagrams of mature oocytes of *Melecta albifrons albovaria* and *Xeromelecta californica*, respectively, lateral views drawn to same scale.

Youssef (1968) reported similar observations for *M. pacifica*, *Xeromelecta californica*, and *Zacosmia maculata*, as did Torchio and Trostle (1986) for *X. californica*. Because of the small size of the hole in the cell cap reported for most of these species, it seems likely that these bees use the apex of their metasoma to punch through the closure. In the case of the unknown species of *Melecta* discussed here, the outer part of the closure did not reveal exterior evidence of the hole through which the eggs had been inserted, and no mention of this was made by Thorp, Torchio and Youssef, or Torchio and Trostle with respect to the melectines they studied. However, one of us (J.G.R.) made observations on *X. californica* attacking nests of *Anthophora occidentalis* Cresson (adults kindly identified of Robert W. Brooks, University of Kansas) at Cedar Point Biological Station, University of Nebraska, north of Ogallala, Keith Co., Nebraska, July 12–19, 1988. From J.G.R.'s unpublished preliminary manuscript, the following is excerpted: "Egg insertion holes were discovered on the inner surfaces of the cell closures of 15 cells . . . . In only two of the cells was the hole seen to penetrate to the outer surface, an indication that the female cuckoo [bee] usually patches the hole on the outer surface after oviposition . . . . In most (but not all) parasitized cells, a large depression 4–5 mm wide and 2–3 mm deep, sometimes accompanied by scratch marks, occurred on the outer surface, indicating that the *Xeromelecta* female first made a depression with her mandibles before drilling (or punching) a small hole less than 1.0 mm in diameter through [the cell closure] to the cell lumen, presumably with the tip of her metasoma." Samples of these cell closures are in the collections of the American Museum of Natural History. Such variable behavior may depend on whether the cell closure material is still moist from construction so that it can be easily reinstalled by the female cleptoparasite after she oviposits. However, the observations do seem to suggest that the cleptoparasite can oviposit in nests where the cell closure has already dried after being constructed by the *Anthophora* female.

Unexplained for any melectine is how the ovipositing female manipulates the apex of her metasoma to attach the egg to the cell closure some distance (in the case of our observation, 3.0 mm) from the hole in the cell cap and by what means the posterior end of the egg adheres to the closure.

The following description is based on field notes made at the time of finding the egg attached to the cell closure. It was allowed to dry, still attached, so that pictures could be taken of it relative to the insertion hole (figs. 60, 61). Subsequently, the shriveled egg was removed and studied by SEM.

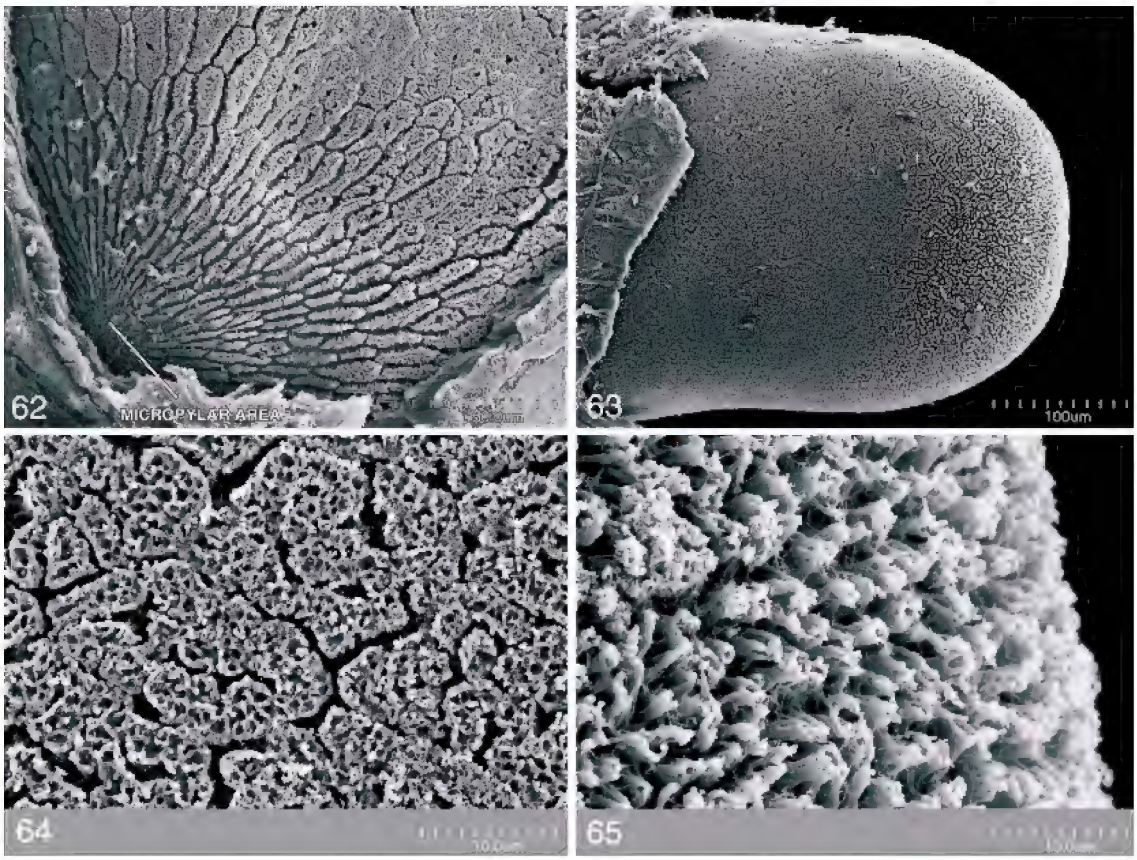
EGG (figs. 56–58, 60, 61): Length 3.0 mm; maximum diameter 0.64 mm; size relative to intertegular distance unknown because female not collected. Shape elongate, approximately symmetrical around its moderately curved long axis; anterior and posterior ends rounded; maximum diameter near anterior



Figs. 54–59. **54, 55.** SEM micrographs of anterior pole (frontal view) and posterior end (lateral view) of mature oocyte of *Melecta albifrons albovaria*, showing chorionic ornamentation. **56–58.** SEM micrographs of dried egg of *Melecta* species. **56.** Anterior end of egg with micropylar area identified by large rectangle. **57.** Close-up of micropylar area of fig. 58; note unexplained apparent absence of pores. **58.** Close-up of area of chorion identified by smaller rectangle in fig. 58, showing grooves bordering polygons. **59.** Anterior end of mature oocyte of *Thyreomelecta kirghisia*, showing polygonal pattern around micropyle and farther back, anterolateral view.

60

61



Figs. 62–65. SEM micrographs of mature oocyte of *Xeromelecta californica*. **62.** Anterior end showing polygonal pattern around micropylar area, lower left corner. **63.** Posterior end of oocyte. **64.** Chorionic patterning between near posterior end. **65.** Chorionic patterning at extreme posterior end. Figs. 64 and 65 to same scale.

end, gradually tapering to other end; micropyle not evident under stereomicroscopic examination; under SEM (figs. 56–58), micropylar area easily identified (figs. 56, 57) but pores not certainly seen; area covered by sculpturing that seems to lead to one edge of the elliptical micropylar area. Chorion smooth, opaque, dull, and white, lacking sculpturing and other ornamentation as seen by stereomicroscope; under SEM (figs. 56–58), anterior end with strong polygonal pattern created by grooves in chorion, the polygons becoming more elongate toward anterior pole; this pattern bilaterally symmetrical, not radially symmetrical (fig. 56).

MATERIAL STUDIED: One egg, Turkey: Erzurum: 22 km WSW Oltu, VI-25–2001 (J.G. Rozen).

REMARKS: The difference from the oocyte of *Melecta albifrons albovaria*, described above, and the egg of *Melecta* sp. is slight and pertains only to the subtle interpretation

←

Figs. 60, 61. Macrophotographs of ovipostion site of *Melecta* species on inner surface of closure of vertical cell of *Anthophora* (*Lophanthophora*) nr. *fulvitarsis*, entire closure and close-up views, respectively, showing shriveled white egg of *Melecta* species, attached to the closure by its posterior end, left, close to the closure perimeter, and two oviposition holes. Posterior end of egg at far left, 3 mm from closest insertion hole. Cell closure 9.0 mm in diameter. For further details, see text.

of the position of the widest diameter; this egg may well be that of *M. albifrons albovaria*, the most common of the three species of *Melecta* found at the site.

Thyreomelecta kirghisia Rightmyer and Engel

MATURE OOCYTE (fig. 59): Length 1.95–2.35 mm; maximum diameter 0.35–0.45 mm; egg index 0.68 (small). Shape as described for *Melecta albifrons albovaria*; micropyle not evident under stereoscopic examination; under SEM examination, micropyle almost certainly at anterior pole (fig. 59). Anterior chorion with polygons becoming narrower the closer they are to micropyle, very much as in *M. albiforns albovaria*, with these polygons identified by grooved borders; chorion elsewhere not observed.

MATERIAL STUDIED: One female, Kyrgyzstan: Issyk-kul, S shore Issyk Kul, 10 km E Kadzhi-Saj, 1675 m, 42°10′33″N, 77°18′55″E, VII-03–1999 (J.G. Rozen).

REMARKS: This female was collected with the type series of the species.

Because of the difficulty of removing mature oocytes of melectines from their ovarioles, the chorion of this species was observed on the anterior end of only one oocyte. Its polygonal patterning, though similar to *Melecta albifrons albovaria*, was not as pronounced, possibly a result of not being fully deposited. Further, the micropyle was not fully exposed.

Thyreus lieftincki Rozen

The egg and egg deposition habits of this species were described by Rozen (1969). Two eggs from that study were preserved and have an average length of 3.53 mm. However, Rozen (1969) stated that five eggs ranged in length from 3.5 to 3.75 mm, which gives a median of 3.63 mm. To calculate the egg index of this species, we measured the intertegular distance of the holotype and the two other known females (paratypes), which averaged 4.29 mm. The egg index based on the two preserved females is 0.82, and based on the median value calculated from the range of lengths of five eggs is 0.84, both medium in the classification of Iwata and Sakagami (1966). These indices are close to 0.85, reported by Iwata and Sakagami (1966) for *Thyreus japonicus* (Friese).

The specimens, preserved in Kahle's solution, are in fair condition, too poor to be illustrated. The only information to add to the original description is that the chorion is dull. There are no features that seem to distinguish them from the eggs of other Melectini.

MATERIAL STUDIED: Two eggs, Republic of South Africa: Cape Province, 3 mi S Avontuur, XI-15–1966 (J.G. Rozen).

Xeromelecta californica (Cresson)

The egg of this species was previously described by Torchio and Trostle (1986).

MATURE OOCYTE (figs. 62–65): Length 1.70–2.95 mm; maximum diameter 0.35–0.48 mm; egg index 0.59 (small). Shape as described for *Melecta albifrons albovaria*; micropyle at anterior pole (fig. 62), not on a pronounced projection, apparently similar to that of egg of *Melecta* species described above, with area around it consisting of elongate converging polygons (fig. 62), borders of which are defined by grooves. Chorion (figs. 64, 65) similar to that of *Melecta albifrons albovaria* except polygons of midbody scarcely visible, and slight differences in ultrastructure of truncated projections.

MATERIAL STUDIED: Two females, Nebraska: Keith Co., Cedar Point Biological Station, VII-8–1987 (J.G. Rozen) near site of *Anthophora occidentalis*; same except VII-19–1988, from cells of *A. occidentalis*.

REMARKS: The egg deposition habits of this species are discussed under *Melecta* species, above.

One of the females collected in 1988 contained no mature oocytes, no doubt because it had recently emerged from the pupa. All ovarioles were in an equal state of development, with the comparable oocytes in ovariole series equal in size. Among the three females with mature oocytes, there was a surprising range in the egg index from 0.40 to 0.73.

DISCUSSION

As pointed out first by Iwata (1955, 1960, 1964) and Iwata and Sakagami (1966), mature oocytes/eggs of cleptoparasitic bees tend to be smaller than those of related nonparasitic taxa, a conclusion supported by numer-

ous subsequent studies (Alexander, 1996; Alexander and Rozen, 1987; Alves-dos-Santos et al., 2002; Garófalo and Rozen, 2001; Roig-Alsina and Rozen, 1994; Rozen, 1986a, 1992, 1994b, 1997, 2001; Rozen and Roig-Alsina, 1991; Rozen and McGinley, 1991; Rozen et al., 1997) as well as by the taxa dealt with here. However, as demonstrated by this paper, cleptoparasitic bees have other egg features that often distinguish them from nonparasitic forms; they show great variation in their micropylar structure, dimensions, and chorionic ornamentation, thickness, and patterning. This variation appears far greater than that known among nonparasitic taxa.

We strongly suspect that the extreme variation in parasitic eggs is restricted to those taxa that introduce their eggs into cells that are still open, presumably being provisioned by host females (to be discussed more broadly in a subsequent study by Rozen, in press). Thus, we see great variation in the mature oocytes of the Nomadinae, all members of which are thought to enter host cells that are open, and little variation in the eggs of the Melectini, which are inserted into sealed cells and retain a form similar to that of host eggs. As hinted above, the peculiarly sculptured egg of *Dioxys cincta* may be an indication that it is introduced into an open host cell whereas those of North American congeners are inserted into closed cells.

We make special note of the extreme variation found among the mature oocytes/eggs of the Ammobatini. We think that this variation is driven by strong selection pressure favoring hiding of eggs from returning host females, although exactly how this is accomplished by the huge opercular area of *Ammobates carinatus* contrasting with the flat, ebony operculum of *Parammobatodes rozeni* is unknown. Similarly, we wonder why within the genus *Oreopasites* so many kinds of opercula have evolved. This we interpret as evidence of strong selection pressure, but we are left with the intriguing question why does not one kind of ornamentation fit all?

ACKNOWLEDGMENTS

The first author expresses his sincere appreciation to Robert G. Goelet, Chairman Emeritus, Board of Trustees, American Museum of Natural History, for supporting the fieldtrip leading to this investigation. We express our thanks to: Michael S. Engel, University of Kansas, for the identification of "*Parammobatoides*" *orientana* and the melectines associated with this study; Robert W. Brooks, University of Kansas, for determining the *Anthophora*; Yuriy A. Pesenko, Russian Academy of Science, St. Petersburg, for the identification of the host of "*Parammobatoides*" *orientana*; and Maximilian Schwarz, Ansfelden, Austria, for identifying, describing, and naming *Parammobatodes rozeni*, the description of which is appended below.

We thank the following Scientific Assistants at the American Museum of Natural History who provided substantial assistance and expertise to this project: Tam C. Nguyen took the macrographs of the oocytes; Steve Thurston photographed the cell cap punctured by *Melecta*; and Valerie Giles was responsible for the numerous SEM micrographs. Steve Thurston also prepared the presentation of all illustrative material, and Eric Quinter, as usual, kindly reviewed the completed manuscript.

Lastly,we express our appreciation to two anonymous reviewers whose thoughtful comments and suggestions improved the final version of the manuscript.

APPENDIX

Parammobatodes rozeni, a new bee species from Israel (Hymenoptera: Apoidea: Apidae: Nomadinae)

by

Maximilian Schwarz[3]

Figures 66–81

Abstract

A new species from Israel, *Parammobatodes rozeni*, is described and compared with its nearest relative, *Parammobatodes nuristanus* Warncke, 1983.

Parammobatodes rozeni, new species

This new species closely resembles *Parammobatodes nuristanus* Warncke in having elongate mouthparts, an elongate labrum, and a relatively

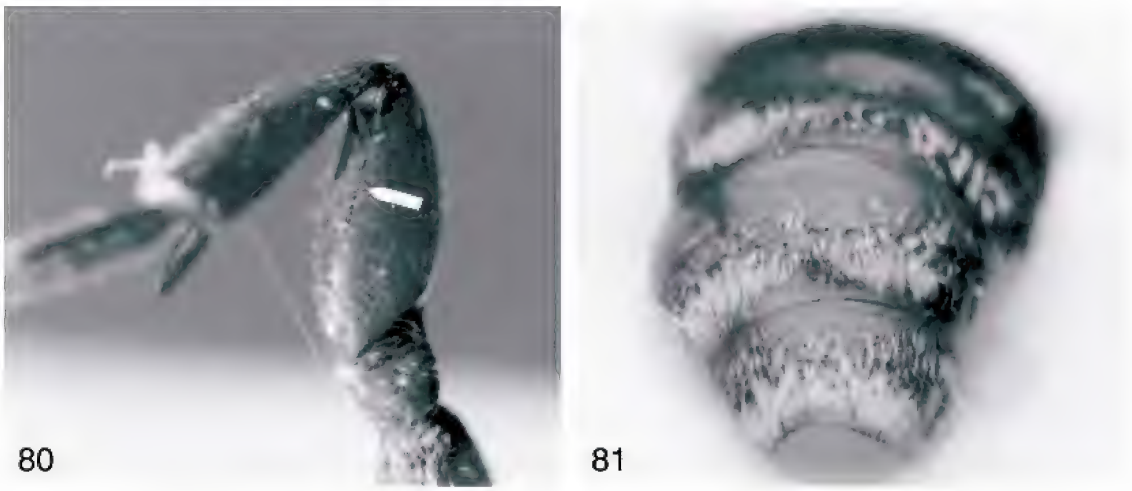
Figs. 66–73. **66–69.** *Parammobatodes rozeni* female. **66.** Labrum laterally. **67.** Labrum dorsally. **68.** Antenna from left. **69.** Frons sculpture. **70–73.** *Parammobatodes nuristanus*, female. **70.** Labrum laterally. **71.** Labrum dorsally. **72.** Antenna from left. **73.** Frons sculpture.

Figs. 74–79. **74–76.** *Parammobatodes rozeni*, female. **74.** Vertex. **75.** Mesoscutum. **76.** Pygidial plate. **77–79.** *Parammobatodes nuristanus*, female. **77.** Vertex. **78.** Mesoscutum. **79.** Pygidial plate.

large second submarginal cell. It is easily distinguished by a different labrum, shorter antennae, and different sculpturing.

Female. Mouthparts long, extending to base of midcoxa when head in normal position, mandibles closed.

Labrum 1.5 × as long as wide, basal two-thirds in profile evenly (almost spherically) convex, api-



Figs. 80, 81. *Parammobatodes rozeni*, female. **80.** Hind femur. **81.** Tergal fasciae.

cal third conspicuously concave, saddlelike (fig. 66), basal half with a few, sparse punctures (fig. 67). (In *P. nuristanus* labrum slightly longer, with basal and apical halves in profile straight and meeting at obtuse angle [fig. 70], basal half finely, relatively densely punctate [punctures 1.0–1.5 diameters apart, interspaces smooth] [fig. 71].)

Antenna short (fig. 68), length of flagellomere I 1.16 × width, length of flagellomere II 0.7 × width, equal to 0.64 length of I. Flagellomere III wider than long (9.5:8), IV as long as wide (9.5: 9.5), V slightly longer than wide (9.75:9.5), and VI even more so (10:9.5). (In *P. nuristanus* antenna slightly longer [fig. 72], with flagellomere I inconspicuously longer than wide [11.5:11] and only 1.27 × as long as II, the latter 1.27 × as wide as long [11.5:9], flagellomeres III and IV slightly longer than wide (11:10.5), III being as long as 1.22 of II, V and VI becoming gradually longer, V 1.09 × as long as wide, VI 1.14 × as long as wide.)

Punctures of upper frons (beneath midocellus) several diameters apart, interspaces shiny, unsculptured (fig. 69). (In *P. nuristanus* punctures of upper frons less than one diameter apart [fig. 73].)

Vertex conspicuously shiny between hind ocellus and orbit, finely, sparsely punctate, with no differentiated area next to hind ocellus. Interocellar area almost impunctate (fig. 74). (*P. nuristanus* with large, conspicuous, shiny area next to hind ocellus at least as large as hind ocellus; punctures between ocellus and orbit somewhat denser and as large as those on front, on interocellar area dense, somewhat finer than on frons [fig. 77].)

Mesoscutum mesally with conspicuous, longitudinal impression that has a fine furrow at bottom and extends from posterior margin of pronotum almost to anterior margin of scutellum, gradually merging posteriorly into mesoscutal convexity. Mesoscutal punctures, on each side of impression, very sparse, a little smaller than those on frons (fig. 75). (In *P. nuristanus* mesoscutum uniformly convex, mesally with well-defined, longitudinal furrow; punctures, on each side of furrow, denser and as large as those on the frons; fig. 78.)

Punctation of terga minute, sparse. (Even more so than in *P. minutus* (Mocsáry).)

Pygidial plate slightly narrower than in *P. nuristanus*, punctures finer, sparser, and light setae, particularly laterally near apex, slightly longer, more erect (fig. 76). (In *P. nuristanus* plate relatively wide, basally with relatively large, dense punctures and small interspaces, apically with very short, appressed, dense setae; lateral setae short; fig. 79.) Hind femur overall as in *P. nuristanus*, ventral margin of posterior surface sharply carinate (fig. 80).

Head, mesopleuron, and propodeal side with silvery, dense, appressed setae, sculpturing recognizable from certain angles on clypeus, frons, and vertex. Scutal margins and propodeum with appressed, silvery setae. Terga III–V each with wide, uninterrupted, silvery fascia of appressed setae, each fascia also with erect, light setae (fig. 81). Overall body pilosity as in *P. nuristanus* (Warncke's [1983:281] description of setae is either incorrect or imprecise).

Body predominantly brownish red, but frons, vertex, gena, antenna from flagellomere V on, and mesoscutum black. Overall body color as in *P. nuristanus*, except head, thorax lighter red in latter species and antenna all red.

Length 6.0–7.0 mm.

Male unknown.

The new species is named in honor of Jerome G. Rozen, Jr.

Holotype: Female, Israel: [Hadarom] S Negev 15 km N Shizzafon Junction [30°02′30″N, 35°01′40″E], 9 May 1997, J.G. and B.L. Rozen (Tel Aviv University).

Paratype: Female, same data as holotype (M. Schwarz collection).

COMMENT

Both specimens examined were preserved in Kahle's solution for a study of oocytes and ovaries. As they were not recognized as a new species at the time of dissecting, no particular attention was paid to their condition. The fresh specimen, the paratype, was dissected, with the well-preserved body parts, the gastral apex, and the left hind leg mounted separately on a piece of cardboard. The holotype is worn, with pilosity of the head and apical fasciae of terga III–V particularly affected (these fasciae are well preserved only laterally, although the long, light, erect setae are well preserved.) The fascia of tergum V is somewhat worn off mesally.

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